Barley Yellow Dwarf, A Virus Disease of Cereals and Grasses

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INTRODUCTION

Barley yellow dwarf has been recognized as a virus disease of cereals and grasses only since 1951, when it was discovered by Oswald and Houston (164) in California. Nevertheless, even in this short time it has become accepted as a disease of major importance in many areas of the United States, and in other countries as well. In 1959, for example. barley yellow dwarf virus incited the most serious single disease of oats in the United States and caused production losses in the central oat belt comparable with those recorded for various epidemics of other major diseases of that crop (156, 157). Moreover, inherent in the economic implications of barley yellow dwarf is the long-range potential of a disease that is caused by a versatile virus of wide host range. Even in its infancy, therefore, barley yellow dwarf seems destined to assume classic status among cereal diseases and thus to become increasingly important in teaching and research. Hence, there is compelling need for monographic treatment of this disease at this time, to provide both a teaching aid and a standard reference for the rapidly increasing diverse research activity.

Throughout the manuscript, the author uses the terms cereals and small grains. These words are meant to refer only to barley, oats, wheat, and rye in this treatise. Also, considerable detail of aphid life cycles is included in the belief that, as the only means of spread of the barley yellow dwarf virus, any factor affecting the aphid is important to the disease.

Name.—Barley yellow dwarf was the descriptive name first applied to this disease by Oswald and Houston (164). Hence, according to the practices of nomenclature followed in the United States, barley yellow dwarf is the correct name of the disease and the virus that causes it is barley yellow dwarf virus. The virus name includes the name of the first known major host (barley), a descriptive word or phrase (yellow dwarf). and the word virus. in that order. In keeping with accepted practice, therefore, barley yellow dwarf (BYD) and barley yellow dwarf virus (BYDV) are now widely established in the literature as the correct names of the disease and the virus on all cereal and grass hosts. For example, despite its characteristic symptoms, infectious "red leaf" of oats is called yellow dwarf, because it is caused by the BYDV (7. 200, 237, 238).

The names, cereal yellow dwarf and cereal yellow dwarf virus, were preferred by many workers (45, 46, 166. 168, 244) because of the importance of the disease on hosts other than barley. Consequently, these technically invalid synonyms were widely used. For convenience, it is permissible to refer simply to yellow dwarf in an individual paper after the subject has been established. However, the unmodified designation, yellow dwarf, should never be used in titles because of possible confusion with other yellow dwarf diseases (onion, tobacco, potato).

Klinkowski and Kreutzberg (137) used the name *Hordeumvirus nanescens*, literally, the "barley dwarfing virus." The use of binomials might have merit, since this would aid in establishing the identity of the virus. Rademacher and Schwarz (184) used the binomial *H. nanescens* in the title of their paper on the red leaf disease of oats, thus making it clear that the subject was yellow dwarf of oats.

Discovery of Barley Yellow Dwarf.—About mid-April, 1951 (168) barley in the vicinity of Davis, Calif. turned yellow within a week. By May 1, reports of a severe yellowing and stunting of the crop had come in from practically the entire state. These symptoms were similar to those sometimes attributed to nutrient deficiencies. However, the widespread distribution of the disease covered areas of diverse moisture and temperature conditions. and soil conditions that varied over a wide range of pH, nitrogen levels, salinity, etc. Consequently, this sudden widespread diseased condition could not logically be attributed to a nutrient deficiency, especially since the most brilliantly yellow barley occurred, in many cases, on the most fertile soils.

The occurrence of stunted and yellowed plants side-by-side and intermingled with apparently normal plants provided strong evidence that the disease was not the direct result of an imbalance in soil fertility or of unfavorable weather conditions. This intermingling of healthy and diseased plants, along with the sudden appearance of the yellowing symptom over a large area, indicated the action of something infectious. Root rot was suspected but no constant associations could be established between root-rot fungi and the sick barley. Furthermore, it was unlikely that root rot could have become epidemic in this fashion. Injury from aphid feeding was also considered; and, although aphid populations in the grain fields were higher than normal, these populations were not high enough to cause the trouble directly.

The above sequence of observations led Oswald and Houston (164) to move aphids from diseased plants to healthy seedlings, which also began to exhibit disease symptoms in 2-3 weeks. With further refinement of experimental procedures, these results were verified and the cause of the California epidemic in barley was established as a new virus disease of barley with aphid vectors. The disease was called yellow dwarf, a name descriptive of the symptoms on barley, the major host in California.

The same virus was simultaneously proven to be the cause of a reddening of late-sown spring oats and a yellowing of late-sown spring wheat, also common in California that year (167).

Following its discovery in 1951, barley yellow dwarf was identified in such widely separated localities as Minnesota (153) and Arkansas (203) in 1952, in Mississippi (230) and Iowa (267) in 1953, and shortly thereafter in several other states. As a new disease, not seed-borne, it is unlikely that it could have spread so rapidly from a single focal infestation.

As an old disease on major crops that receive the perennial close scrutiny of plant pathologists, it seemed incredible that it could have been overlooked for long. And yet, Oswald and Houston (168) doubted that it was new to California. They believed it had been previously observed in California but only as an unknown disease of little consequence on scattered plants. Its occurrence in epidemic form led to the discovery of its true cause and to its current widespread recognition as a disease of major importance.

Moreover, there is good circumstantial evidence that yellow dwarf is a disease of long standing in several cereal-producing areas of the United States, southeastern Canada, and Europe, rather than one that has spread rapidly from California in recent years. There is evidence of major epidemics in the United States prior to the establishment of its identity as a virus disease. The literature abounds with reports of cereal disease epidemics of unknown cause that were, in all likelihood, epidemics of yellow dwarf. "Red leaf" of oats is the best documented example.

Some Pre-1951 Observations.—In the light of current knowledge, many of the early accounts of widespread red leaf of oats can be interpreted logically as accounts of yellow dwarf epidemics. T. F. Manns (144) gave an exhaustive and detailed account of early observations of red leaf of oats in the United States in "The blade blight of oats, a bacterial disease." Manns explained that this widespread condition was due to a simultaneous infection by 2 bacteria in a symbiotic relationship, aided by cloudy, rainy, humid weather. The subsequent failure of pathologists to recognize such a bacterial disease leaves his hypothesis of etiology open to doubt. The documentation and description in this work are valuable as possible evidence of widespread yellow dwarf of oats prior to 1909, and the following observations are taken largely from his bulletin.

According to Galloway and Southworth (108), a severe, mysterious malady of oats developed in 1890 from New England to Georgia and westward to Indiana and Illinois. The oats tillered poorly, were short, diseased on all manner of soils, and no animal or fungal parasites were found to explain the trouble. Manns (144) noted that Thaxter in Connecticut in 1889 reported a reddening of oats, not a rust, in which the plants matured little of their seed. In 1907, Thorne (144) reported from Ohio that "In the present attack plant lice (aphids) have been mentioned by many observers as being unusually abundant on oats, but we have not as yet found conclusive evidence as to whether they have or have not borne an important part in the spread of the trouble." Gossard (144), also in Ohio in the same year, noted the abundance of the English grain aphid [*Macrosiphum granarium* (Kirby)] and thrips on oats, but concluded that the real cause of the oat malady was the cold, wet spring.

The numerous references to aphids led Manns to take English grain aphids from blighted oats and cage them on healthy seedlings. "Ten to twelve days after the caging the blight began to show, while the check outside the cage remained free" (144, p. 111). In the legend for Plate XI, page 150, he again reported that aphids could spread the disease, but his experiments and observations led him to believe the aphids acted as vectors of bacteria.

Manns, in summarizing his own observations of the epidemic of 1907, stated that in advanced stages, oat leaves could be as red as fire and that blast, or sterility, was proportional to the leaf blight. On close examination, the blast was not attributed to direct bacterial attack, but to some over-all lack of vitality occasioned several weeks before the emergence of the panicle. The blight was influenced little by soil fertility or drainage. It was reported from the Canadian Lake Provinces to the Gulf States, and from the Atlantic to Illlinois, depending on the season.

According to the Manns review (144), the 2 years of greatest damage were 1890 and 1907; the latter was the more serious. It seems more than merely coincidental that Webster and Phillips (263), in their treatise on the greenbug [*Toxoptera graminum* (Rond.)] reported that 1890 and 1907 were years of greatest greenbug spread, especially since the spread was greater in 1907. It seems further significant that in their studies of the influence of weather on aphid biology they found that conditions in 1890 and 1907 were particularly adverse to the natural enemies of aphids in the spring months.

Elliott (79) doubted the bacterial hypothesis advanced by Manns (144), and stated that Manns, in all probability, had described a disease other than halo blight. Elliott was unable to isolate pathogenic bacteria from reddened oat leaves from Wisconsin that were quite like those illustrated by Manns.

A possible case of barley yellow dwarf, designated as "red blade" of oats, was recorded in a plant disease survey in the state of Washington, dated 1918. The diseased condition prevailed in oats west of the Cascade Mountains and was found to a lesser degree in eastern Washington. The cause was listed as low temperatures during early development of the plants. Some years later, a similar oat malady was reported by Sprague (226, 227) as a prevalent and disturbing condition in Oregon. It was serious in the Willamette Valley and Coast regions in all oats, whether fall-, winter-, or spring-sown. In 2 counties east of the Cascades, Sherman and Wasco, the disease was present only in spring oats.

Sprague stressed the fact that red leaves as such, without more critical description, do not indicate a specific disease. Contributing factors in Oregon were heavy rains, water-logged soils, high carbon dioxide content of soils, and leaching (227). High soil acidity was particularly injurious during winter months. Chloroplasts were probably injured by low temperatures, as the reddening was most noticeable in fall-sown, non-winter-hardy oats of the red oat group. An open winter had favored top growth in excess of root development in cold wet soils. *Fusarium culmorum* (W. G. Smith) Sacc., attacking root and crowns, caused reddened leaves. Sprague (228) also found a leaf-spotting fungus capable of causing a red, leathered condition of the leaves in oats [*Spermospora avenae* (Sprague & A. G. Johnson) Sprague]. This

condition, called leather-leaf, is most obvious in February, and the plants usually recover with the arrival of warmer weather.

Sprague's observations suggest that red leaf in oats has numerous causes, of which those he lists help explain some, but not all, red leaf of oats in the Pacific Northwest. It is now an established fact that most red leaf persists in spring oats in May, June, and right up to loss of color at maturity in a wide range of temperatures and over all manner of soil conditions in the Pacific Northwest. Usually, before June, all traces of water-logging have disappeared from agricultural soils of this region, but oats seldom recover from the earlier prevalent red leaf condition.

In 1937, Barrus (22) described a red leaf disease of oats prevalent and long known in New York. In that year, reddening appeared even before the oats had stooled. It was not restricted to plants in low spots or in dead furrows, but was scattered, either on individual plants or on several adjacent plants, along the drill row. These plants remained short and there was a high degree of sterility, or blasting, of spikelets that was correlated with the degree of leaf reddening. The blades remained rose red, violet red, or purplish. The reddening was limited to the oldest living leaves. Barrus found no evidence that root-rot or leaf-spotting fungi were possible causes, although the spring of 1937 was marked by heavy rains, so that many fields were sown late. The symptoms and field occurrence of the disease, as reported by Barrus, are remarkably similar to Oswald and Houston's (167) later description of yellow dwarf.

Today, it appears that barley yellow dwarf is not new in the United States. The descriptions of epidemics of a red leaf condition of oats associated with blasting of florets; the frequent references to late seeding following cool, wet springs; the numerous references to abundant aphid populations in the years of epidemics; and the failure of most observers to associate the disease with soil conditions or specific pathogens—all strongly suggest yellow dwarf on that host. The discovery by Oswald and Houston (164, 168) that yellow dwarf is a virus disease of cereals and grasses is one of the major contributions in cereal pathology of recent decades.

Rademacher and Schwarz (184) report that, as in the United States, yellow dwarf is not new in Germany. As early as 1929, Rademacher (183) studied a red leaf condition in oats and a sterility associated with it. No pathogen could be associated with the disease; and, in 1946-47, it was demonstrated not to be seed-borne. After the discovery of yellow dwarf as a virus disease in California, the long-recognized malady of oats in Germany was proven to be the same disease (184).

Cereal Diseases Similar to Barley Yellow Dwarf.—Virus diseases of cereals are being rapidly discovered, and already several are recognized in the Western Hemisphere that are similar in some aspects to barley yellow dwarf. Some are known to be different, while others might be the same. One such disease is a severe "oat chlorosis," or "yellow leaf" of oats, reported by Farrar and Gore (99) in Georgia. In 1958, Farrer (97, 98) reported transmission of a virus by the apple grain aphid, from yellow leaf diseased oats to healthy oats and barley. The description of the disease and its field characteristics are indistinguishable from those of yellow dwarf on oats, except that yellow is the major color symptom. It was particularly widespread on the oat variety Victorgrain 48-93. Byrd, Earhart, and Eskew (50) noted what might be the same malady in South Carolina, particularly on Victorgrain 48-93, although they did not determine the etiology of the chlorosis. If the yellow leaf condition of oats in Georgia and South Carolina is yellow dwarf, it probably is caused by a strain of the virus that differs from the BYDV strains of most regions. In Mississippi, Rothman, Bowman, and Ivanoff (205) found color in diseased oats ranging from blue-purple to red or yellow. Specimens of each type of discolored oats were sent to Rochow (205), who recovered the BYDV from all 3 types.

Bruehl and Damsteegt (unpublished) grew 3,600 varieties of the world spring oat collection of the U.S. Department of Agriculture at Vancouver, Wash., in 1959 in an epidemic of yellow dwarf. Colorations of diseased plants of the vast majority consisted of a blending of red, crimson, salmon, and yellow when the oats were still in a condition of some vitality. When an oat variety appeared to deviate significantly from this interblending of the usual colors, it was recorded. Thirty-five oats were classified as salmon-yellow, 4 as bleached salmon, 4 as yellow-salmon, and only 6 were noted in which yellow was the dominant color (C.I. No. 1537, 1651, 3798, 5326, 6760, and 7282). Only 1, the variety Golden, C.I. 6760, was a true yellow. This would indicate that the marked yellowing in the southeast, if due to yellow dwarf, is indeed the result of a distinct strain of the virus. Victorgrain 48-93 was in this nursery and its reaction was typical of most varieties (*i.e.*, red-purple-salmon).

Enanismo (110, 111), a disease of barley, wheat, and oats occurring in Colombia and Ecuador, somewhat resembles BYD. It occurs when field-collected leafhoppers (*Cicadulina pastusae* Rup. & DeL.) are fed on host plants. The symptoms on barley, wheat, and oats are similar to those of BYD. The association of this disease with the feeding of a leafhopper suggests that it is, in all likelihood, a different disease.

In 1952, Moore (153) reported aphid transmission of red leaf and possible, but not certain, transmission of a blue dwarf of oats by the apple grain aphid. In 1954, Sill, King, and Hansing (216) noted a blue dwarf and red leaf of oats in Kansas. Confusion existed because BYD in severe form can cause symptoms resembling the descriptive term "blue dwarf," *i.e.*, severe stunting and deeper green than normal, or a bluish green. The blue-dwarf, red-leaf puzzle was solved in 1959 when Banttari and Moore (20) proved that blue dwarf is a distinct and separate disease. Blue dwarf is caused by a virus transmitted by the 6-spotted leafhopper (*Macrosteles fascifrons* Stål). The blue-dwarf virus is pathogenic to barley as well as oats. In 1960, these same workers (21) discovered that, in addition to the oat blue-dwarf virus, *M. fascifrons* transmits the aster yellows virus to barley.

Barley suffering from aster yellows is severely dwarfed with little elongation of internodes and the leaves are rolled tightly backward. The latter symptom is the reverse of an inward, upward-curling tendency sometimes observed in yellow dwarf, particularly of oats.

In China, Yu, Pei, and Hsu (269) described a virus disease similar to barley yellow dwarf, but sufficiently different to class it at least temporarily, as a distinct disease. The virus attacks foxtail (Italian) millet [*Setaria italica* (L.) Beauv.], stunting it and producing a reddening of purple-stemmed varieties and a yellowing of green-stemmed varieties. It is transmitted by the corn leaf aphid, the English grain aphid, and the greenbug, but not by the cotton, peach, or soybean aphids. The foxtail-millet virus persists in its vectors. In addition to Italian millet, its hosts include *Zea mays* L., *Setaria lutescens* (Weigel) F. T. Hubb, *S. viridis* (L.) Beauv., *Digitaria sanguinalis* (L.) Scop., *Echinochloa crus-galli* (L.) Beauv., and *Panicum miliaceum* L. The Italian millets are highly susceptible, as shown by the fact that only 9 of 349 varieties were classified as highly tolerant.

DISTRIBUTION AND ECONOMIC IMPORTANCE

Barley yellow dwarf is now known to be present in 3 continents: North America, Europe, and Australia. It is probable that cereal pathologists in other areas will make the use of "world wide" appropriate in describing the distribution of this disease. In North America, it is known from the Matanuska and Tenana Valleys of Alaska (76); Alberta (219) and Ontario (221), Canada; throughout continental United States (Table 1); and southward to the state of Sonora, Mexico (correspondence with N. E. Borloug). In northern Europe, yellow dwarf has been discovered in Great Britain (220, 254, 255), The Netherlands (169, 220, 268), Norway (220), Sweden (140), France (220), Finland (220), and Germany (184, 220). It has been reported from New South Wales, Australia (49, 223), Tasmania, and New Zealand (223). This is an impressive record of discovery in the short time this disease has been known. BYD will probably eventually be established as the most widely distributed virus disease of the Gramineae.

The known distribution of a disease is only dependent upon reports of its identification in diverse areas. Valid estimates of economic importance, however, depend upon extensive observations over a period of seasons. In most areas, the experience of plant pathologists with barley yellow dwarf is too limited to permit a sound estimate, but enough is known to remove all doubt that yellow dwarf is a disease with which to be reckoned, at least in the United States (Table 1). Murphy (156) states that the yellow dwarf epidemic of 1959 on oats in Midwestern United States was a major factor in the low production of that crop, making it comparable to Victoria blight and crown rust in its destructiveness. In England (254) yellow dwarf was primarily of "academic interest" until a mild winter (1956-57) was followed by the earliest and greatest migration of grain aphids known, and concurrently by a general outbreak of BYD. This infestation continued, involving fall-seeded grain of

TABLE 1. Known distribution and some observations suggesting the economic importance of barley yellow dwarf in the United States

Region	Loss estimate
Pacific States	
California	5,540,800 bu barley in 1951 (10% of the crops)[a]; also important in oats and wheat (167)
Oregon	$1-3,000,000 combined annual losses in oats, wheat, and barley; more when epidemic east of Cascade Mountains (106, 187)
Washington	$1,000,000 combined annual loss in oats, wheat, barley; more when epidemic east of Cascade Mountains (43, 45)
Alaska	Prevalent in Matanuska and Tenana Valleys (76)
Mountain States	
Idaho	Major disease (178)
Montana	Locally important (215)
Wyoming	Present (250)
Arizona	Present (7)
Plains States	
North Dakota	Minor (182)
South Dakota	50% of oats, 30% of wheat, 20% of barley in eastern tier of counties, 1959 (158)
Nebraska	Important in oats, 1959 (156)
Kansas	6,504,250 bu oats (25% of crops) lost in 1959 (216)
Oklahoma	Present (156)
Texas	Little loss (17)
Prairie States	
Minnesota	Important (103, 156)
Iowa	32,919,600 bu of oats (15% of crop) in 1949 (267); 26,335,680 bu in 1959 (12% of crop) (41)
Wisconsin	6,459,750 bu of oats (5% of crop) in 1959 (15)
Illinois	Major loss, 1959 (127)
Indiana	13,619,925 bu of oats (27.5% of crop) in 1959 (51)
Missouri	14,219,100 bu of oats (37% of crop) in 1959, but complicated by concurrent bacterial blight (211)

TABLE 1.—Con't.

Region	Loss estimate
Southern States	
Arkansas	Important in oats (203)
Mississippi	Important in oats in 1951 (230) and in 1959 (205)
Georgia	Important in oats (99, 154)
Florida	Minor (142)
North Carolina	Serious in oats in 1959, less important in barley and wheat (119)
Virginia	Present (100)
Maryland	Present (7)[b]
Northeastern States	
Michigan	Important in oats, 1959 (134)
Ohio	Of some importance to oats in 1959 (186)
New York	Widespread on oats (191)
Maine	Moderate importance (27)
Massachusetts	Present (238)

[a] The bushel losses are based upon the % losses given by authorities and the 10-year average (1946-55) yields of the crop in question, taken from Agricultural Statistics 1958, U.S. Department of Agriculture.

[b] H. C. Murphy, in a U.S. Department of Agriculture news release, stated that yellow dwarf was destructive to spring oats in 1960 in Pennsylvania, New York, New Jersey, and Maryland.

1957-58 with serious effects upon yield, particularly of winter oats. In Germany (184), New Zealand (223), New South Wales (49), and Canada (221, 222), losses have not been great, but they were adequate to stimulate investigation and inclusion of BYD within the cereal pathology programs of those countries. In addition to bushel losses, there are losses associated with reduced bushel weights and thin kernels.

An aspect of yellow dwarf that has received essentially no consideration is its influence upon pasture, range, and meadow grasses. Many of the grasses are fully as susceptible as the cereals; and infection by the BYDV would greatly reduce the productivity, both of forage and seed, of such grasses. Susceptible grasses are probably eliminated as being "unadapted" to areas such as western Oregon and Washington where escape for long is almost impossible. The longevity of grasses—their ability to tolerate drought, cold, grazing, and other adversities—surely is affected. This neglected phase of the disease should be investigated.

HOST RANGE

The barley yellow dwarf virus has the advantage of a wide diversity of hosts among the Gramineae. Following their discovery of barley as a host of the BYDV, Oswald and Houston (168) extended our knowledge of the host range to include wheat, oats, and many grasses, including perennials as well as annuals. Among them were widely distributed lawn, weed, pasture, and range grasses. Some are symptomless carriers of the virus, while others exhibit characteristic symptoms, often fully as susceptible as barley, wheat, or oats. Grass species are so widespread and numerous that, even though limited to them, this virus is assured a variety of hosts wherever its major economic hosts (oats, barley, wheat) are grown. This diversity in host range within the grass family, coupled with the numerous aphid species capable of serving as vectors, each with somewhat different feeding habits and times of flight, admirably adapts the virus for survival.

An important consideration in host range studies of the BYDV is the feeding habits of aphids under natural conditions. They are more selective when free than when confined upon a certain grass as in typical greenhouse experiments. They can be forced to feed, at least for a limited time, upon hosts they would ordinarily reject. When free, the aphid would quickly leave an unpalatable host and seek one more to its liking. As this virus is seldom acquired in feedings of very short duration, unpalatable grasses would not likely serve as sources of virus, even though susceptible. Hence, it is important to distinguish between hosts obtained in greenhouse trials and those obtained in studies of grasses growing in the field. The former studies are of value as indicative of the potential host range; the latter are evidence of the natural host range.

The known potential host range of the BYDV, as determined largely in greenhouse inoculation trials, is presented in Table 2. The most extensive host range studies to date are those of Oswald and Houston (168) in California, Bruehl and Toko (47) in Washington, and Watson and Mulligan (256) in England.

Some of the same species studied in California were included in Washington, and occasionally the results were strikingly different. *Phleum pratense* L. and *Lolium perenne* L., for example. were reported immune in California and susceptible to a Washington strain of the BYDV. Similar differences in host range will be discussed more fully under a later section on differentiation of strains of the BYDV on the basis of differences in host range.

Table 2. Known hosts of the BYDV, listed with their reactions (immune, symptomless carrier, susceptible) and place studied—California (168), England (256), New York (195), and Washington (47)

Host	Reaction: Immune	Reaction: Symptomless carrier	Reaction: Susceptible
Aegilops triuncialis L.			C[a]
Agropyron cristatum (L). Gaertn.	C,NY,W		NY[b]
A. inerme (Scribn. & Smith) Rydb.	W	W	
A. intermedium (Host) Beauv.	W		W
A. trachycaulum (Link) Malte	W	C	
A. trichophorum (Link) Richt.	W	W	
Agrostis alba L. (or *tenuis* (255))	C,W	E	
Alopecurus agrestis L.		E	
A. pratensis L.	C,E,W,	E	
Andropogon barbinodis Lag.			C
Anthoxanthum odoratum L.		C,E	
Aristida oligantha Michx.			C
Avena abyssinica Hochst.			++[c]
A. barbata Brot.			C,++
A. brevis Roth			++
A. byzantina Koch (cultivated red oat)			C,etc.
A. fatua L.			C,etc.
A. ludoviciana Dur.			++
A. nudibrevis Vav.			++
Avena pilosa			++
A. rouse			
A. sativa L. (common white oat)			C,etc.
A. sterilis L.			++
A. strigosa Schreb.			++
A. weistii Stendel			++
Beckmania syzigachne (Steud.) Fernald	W	W	
Bouteloua curtipendula (Michx.) Torr.		C	
Bromus brizaeformis Fisch. & Meyer			W
B. carinatus Hook, & Arn.			W
B. catharticus Vahl	NY		C,W
B. commutatus Schrad.			W
B. erectus Huds.			W
B. inermis Leyss	W,NY	NY	C
B. japonicus Thunb.			W
B. mollis L. (or *arvensis* (256))		NY	C,W, NY,E
B. racemosus L.			W
B. rigidus Roth.			C,W
B. rubens L.			C
B. secalinus L.			W
B. sterilis L.			E,W
B. tectorum L.			C,W
B. tomentellus Boiss.		W	
Chloris gayanu Kunth.		C	
Cynodon ductylon (L.) Pers.			
Cynosurus cristatus L.		E	
C. echinatus L.			C
Dactylis glomerata L.	NY	C,E,W	W
Dunthonia californicu Boland			C[d]
Deschampsia caespitosa (L.) Beauv.	W	W	
D. danthonioides (Trin.) Munro ex Benth	C	W	
Digitariu sanguinalis (L.) Scop.	C		[e]
Elymus caput-medusae L.		C,W	
E. condensatus Presl.	W	W	
E. triticoides Buckl.	W	C	
Festuca arundinacea Schreb.		C,W	
F. elatior L.		W	
F. idahoensis Elmer		W	
F. myuros L.			C
F. ovina L.		W	
F. pratensis Huds.		E	
F. reflexa Buckl.		W	C
F. rubra L.		W	
Gastridium ventricosum (Gouan) Schinz & Thell			C
Hordeum brevisubulatum (Trin.) Lk.		W	
H. bulbosum L.		W	
H. leporinum Link			C,W
H. vulgare L.			C,etc.
H. hystrix Roth.			C
Hordeum brachyantherum Nevski			C
Koeleria cristata L.		W	W
Lolium multiflorum Lam.		C,W	W[f]
L. perenne L.	C	NY	W
L. remotum Schrenk			W
L. temultentum L.			W
Oryza sativa L.			E
Panicum capillare L.		C	
Phalaris arundinacea L.		W	
P. paradoxa L.			C
P. tuberosa L.	W	C	
Phleum pratense L.	C,NY	NY,W	E,W
Poa ampla Merr.	NY,W	NY,W	
P. annua L.		C,E	
P. canbyi (Scribn.) Piper	W	W	
P. pratensis L.		C,E,W	W
P. trivialis L.	E	E	
Secale cereale L.		C	E
Setaria lutescens (Weigel) F. T. Hubb			W
S. viridis (L.) Beauv.	C		W[g]
Sitanion hystrix (Nutt.) J. G. Smith		W	C
S. jubatum J. G. Smith			W
Sorghum vulgare Pers.	C	C	
S. sudenense (Piper) Stapf.		C	
S. halepense (L.) Pers.			[h]
Triticum aestivum L.			C,etc.
T. durum Desf.			++[i]
T. spp.			++[j]
Zea mays L.	C		E

[a] C represents California (168); E, England (256); NY, New York (195); W, Washington (47).

[b] When the same study, in this case NY (195), lists a host in more than 1 disease reaction column, the reaction varied either because of virus strains or host accessions used.

[c] The ++ reaction represents studies by Endo (85) in Illinois and Bruehl and Damsteegt in Washington (unpublished), in which the species given were studied in the field, definite symptoms observed, but no virus-recovery studies made.

[d] From Allen (6).

[e] Result by Orlob and Arny, personal communication.

[f] Rademacher and Schwarz (184) consider *L. perenne* an important source of virus in Germany. Slykhuis (220) found it frequently with marked symptoms in Europe.

[g] Symptoms were produced (marked stunting and purpling) but attempts to recover the virus failed (47).

[h] From Summers and Bowman (230), in Mississippi.

[i] From a nursery in Vancouver, Wash. Symptoms marked but no attempt made to recover virus (Bruehl and Damsteegt, unpublished).

[j] Hybrids between common wheat and *T. durum* Desf., *T. dicoccum* Schubl., *T. dicoccoides* Korn., *T. persicum* Vav., *T. polonicum* L., and *T. timopheevi* Zhuk. were tested for resistance to yellow dwarf at Vancouver, 1959, by Bruehl and Damsteegt. None showed any resistance beyond that of common wheat. These species should be tested individually, but these observations do indicate that susceptibility is widespread within the genus *Triticum*.

Attempts to produce symptoms and recover virus from the following species have failed: *Agropyron amurense* Drobov (47); *A. elongatum* (Host) Beauv. (47); *A. repens* (L.) Beauv. (47, 256); *A. sibiricum* (Willd.) Beauv. (47); *A. smithii* Rydb. (47); *Agrostis exarata* Trin. (168); *A. palustris* Huds. (47); *A. tenuis* (Sibth.) (256); *Alopecurus arundinaceus* Poir (47); *Arrhenatherum elatius* (L.) Presl. (47, 168, 256); *Bouteloua gracilis* (H. B. K.) Lag. ex Steud. (168); *Echinochloa crus-galli* (L.) Beauv. (47, 168); *Elymus canadensis* L. (47); *E. giganteus* Vahl. (47); *E. glaucus* Buckl. (47, 168); *E. junceus* Fisch. (47); *Holcus lanatus* L. (47, 168); *Oryzopsis hymenoides* (Roem. & Schult.) Ricker (47, 168); *Paspalum dilatatum* Poir (168); *Phleum boehmeri* Wibel. (47); *P. phleoides* Karst (47); *Poa bulbosa* L. (47); *P. compressa* L. (47); *Secale montanum* Guss. (47); *Stipa cernus* Stebbins & Love (168).

Data of natural hosts, as determined by recovery of virus from field specimens, are much more limited. Wheat, oats, and barley, with winter and spring varieties and with volunteer grain in the summer, could nurture both virus and aphids throughout the year in some agricultural areas. Rye (168, 222, 238) is a host to many strains, but it has not been known to suffer materially in the field. In most regions, if not all, however, noncereal grass hosts play a role in epidemiology. Among the perennial grasses, *Poa pratensis* has been implicated as an important reservoir host (159, 222, 239). In Ontario, Canada (222), virus was recovered also from *Agropyron intermedium, Bromus inermis, Festuca rubra, Lolium perenne*, and *Phleum pratense. Lolium perenne* is a known carrier also in Washington, Oregon (Raymer, unpublished), and much of Europe (184, 220, 268). *Phleum pratense* is a carrier in England (255). *Dactylis glomerata* is a known carrier in western Washington and Oregon (Bruehl and Raymer, respectively, unpublished). In warm areas, grasses such as *Sorghum halepense* can harbor the virus (230). These few examples show that in nature a wide range of long-lived grasses is infected, and that the virus is in little danger of annihilation through lack of a host.

Short-lived grasses, other than the cultivated cereals, also can be of real importance. *Bromus sterilis* was commonly diseased in England (254) and *B. rigidus* is an important host in California (7). Research determining the virus content of field-sampled grasses should be expanded so that pathologists may better understand the role of the various species in the disease cycle.

Orlob (159) grew dodder (*Cuscuta campestris*) on diseased barley and obtained the BYDV form the dodder by means of the English grain aphid. Dodder, however, was not listed among the hosts.

SYMPTOMS

The lack of such structures and signs as associated with many fungal and bacterial diseases can be a handicap to positive diagnosis of virus diseases. An experienced plant pathologist might have little difficulty in recognizing a true mosaic pattern, but in the yellows type viroses general discolorations (Fig. 1, see p. 16) and stunting of the host are effects that also might result from various adverse chemical and physical environment factors. Resorting to transmission studies, which require maintenance of virus-free aphids, healthy seedlings and at least 2-3 weeks of incubation for routine diagnosis, is impracticable. Consequently, symptoms are especially important to the diagnosis of virus diseases, including yellow dwarf.

A knowledge of general field conditions where the disease occurs, such as fertility level of the soil, is helpful in diagnosis. This kind of information aided Oswald and Houston (164, 167) in diagnosing yellow dwarf in California in 1951. The yellowing of barley in areas of known high fertility levels, along with intermingled healthy and diseased plants suggested an infectious agent, as did the presence of numerous aphids. It should be kept in mind that only 1 aphid is required ot infect a plant with the BYDV, that aphid populations are subject to rapid change, and that by the time a suspected epidemic of yellow dwarf is noted only a few aphids might be present. Three or 4 weeks earlier, there might have been plenty of active aphids to serve as vectors.

In the absence of other possible causes, such as unfavorable growing conditions, discoloration of cereal plants is indicative of yellow dwarf. The discoloration characteristic of BYD usually begins 7-20 days after inoculation. In the development of yellow dwarf symptoms, the green tissues of the older living leaves begin to discolor unevenly along the leaf margins, at the tips, or well within the lamina in blotches. The discolored areas enlarge and coalesce in a basipetal direction. Green islands may be left for a time within an area in the process of discoloring. At this point, those areas not yet yellowed, reddened, purpled (or whatever) may be darker green than normal for a time. The tissues adjacent to the midrib tend to remain green longer than the rest. The youngest leaves usually show no unusual color. At most they might be somewhat chlorotic. The typical brilliant discolorations of yellow dwarf are seen on the older living leaves, except in very late infection, when the flag leaf alone may develop good discoloration. By contrast, in grass mosaics the clearest symptoms are usually seen in the youngest leaves;

older leaves often lose their mosaic appearance completely.

Leaves of diseased plants are altered morphologically as well as in color. When the susceptible host becomes infected in the seedling stage by a virulent strain of the virus, the third or fourth leaf may emerge distorted. It might be curled sufficiently to project at right angles to the plant axis. It may have marginal serrations, sometimes so deep as to "cut" the blade across its entire width. In moderate to severe yellow dwarf development, the leaves are progressively shortened (89, Table 1), narrower than normal, and stiffer than normal for their entire length, projecting at a sharper angle from the stem than healthy ones. These "spear-like" leaves are quite different from the gracefully blending, flexuous leaves of healthy grasses.

Severe yellow dwarf reduces internode elongation to the extent that the heads fail to emerge, particularly in spring barley. This suppression of heading may prolong the juvenile condition. The stunted, leafy plants occasionally survive longer than normal plants and such dwarfed plants resemble a winter cereal grown from spring seeding. Such plants are nonproductive. Furthermore, they tend to perpetuate the virus and aphids longer into the hot dry period of summer. In fact, the corn leaf aphid thrives on stunted barley of this kind.

In studies of pathological tissues, Esau (89) found no evidence of primary stimulatory effects of the yellow dwarf virus upon its host. Tillering is usually reduced or completely suppressed in oat and wheat varieties, but it may be stimulated in severely stunted barleys. On fertile soil with ample moisture, diseased barley plants might develop excessive tillers and abnormal leafiness. In addition to occasional stimulation of tillering, Wit (268) observed small protuberances on the underside of veins of perennial ryegrass (*Lolium perenne* L.) that apparently was infected with the BYDV. This is the only report of such protuberances on any host. The virus in The Netherlands is virulent on ryegrass, and Wit observed this species in a breeding nursery where a great diversity of genotypes was present.

Yield reduction follows reduced tillering, suppressed heading, sterility, and failure to fill the kernels. Inflorescences of diseased plants emerge later, are smaller, and the number and weight of kernels (75, 82, 86, 167, 233) are reduced. Yields are reduced in oats by "blasting," or sterility. Many of the florets emerge from the boot white and bleached, especially the basal florets of the inflorescence. Endo (85) studied the world collection of the U.S. Department of Agriculture and carefully estimated the degree of sterility among the different varieties. Rademacher (184) studied for years in Germany a blast of oats, which he now considers largely the result of yellow dwarf, and noted differences among varieties. This characteristic of the disease on that host crop was so common that it formed an important part of Endo's varietal ratings, along with general discoloration and stunting of the whole plant. Sterility also has been reported in wheat (255).

Most observers have not examined the roots of infected plants. Oswald and Houston (167) and Allen (6), however, found that the root systems of diseased plants were drastically reduced in weight. Esau (88, 89) found that the major internal symptom of yellow dwarf was phloem necrosis, in both shoots and roots. It is conceivable that the roots are deprived of carbohydrates by failure of the phloem to transport the elaborated foods downward. The reduced root system undoubtedly contributes to the reduced size of the plant, and increases the damage from drought during the growing period of the diseased crop (167, 187).

Factors Influencing Symptom Expression. — Wilson and Murphy (267) discovered that shading reduced symptom expression. Oswald and Thung (169) found that in the winter months in The Netherlands, low light intensities inhibited symptoms. The lack of adequate intensities of light has hindered winter studies in the greenhouse in the cloudy, far western regions of the United States. Allen (6) obtained dependable symptom expression by using lights to supplement daylight to provide a minimum of 500-600 ft-c on the cloudiest days. Endo (84) found, in shading experiments, that reduced light lengthened the incubation period and reduced the severity of symptoms. Orlob and Arny (159, 276) used light intensities ranging downward from 5,600 to 600 ft-c and obtained a steady decrease in disease severity with decreased light. Short days also decreased symptom severity.

Wilson and Murphy (267) also noted that when the greenhouse temperatures fluctuated from 75-95°F the discolored leaves turned brown. Endo (84) found that at 88°F no symptoms developed, whereas at 82°, 75°, and 65°F (the lowest temperature studied) symptom development was poor, good, and excellent, respectively. According to Orlob and Arny (159, 276), a range of 16-24°C was favorable for symptom expression, with strongest symptoms in the cool range. Because of the influence of temperature, inadequately cooled greenhouses are of little or no value for yellow dwarf studies in the summer. Cool nights, however, tend to lessen the deleterious effects of hot days on symptom expression.

Field observations established that symptoms are visible below the temperature range (65-88°F) studied by Endo (84). Oswald and Houston (168) examined a planting of barley made in November, 1951, at Davis, Calif., at monthly intervals beginning in January. They found 3-4% of the plants with symptoms in January, 15% in February, and 23% in mid-March, thus demonstrating that naturally diseased plants can be detected during these cool months. The usual mean January temperature at Davis, Calif., is 45°F. (All weather data of the entire manuscript are taken from U.S. Weather Bureau sources.) The author has made many field collections of yellow dwarf in volunteer cereals at Vancouver, Wash., in November (mean November temperature, 45°F). Symptoms of yellow dwarf are visible in winter cereals there throughout the winter where the mean monthly temperatures are: December, 40°F; January,

38°F; February, 38°F; and March, 47°F.

The effect of fall infection on the yields of winter cereals is not well known. Winter oats suffered at least an 80% loss in yield in England according to Marion Watson (254) and comparable losses in Illinois in the trials of Endo and Brown (87). Winterkilling contributed somewhat to the disease loss in Illinois.

Winter wheat in the region of yellow dwarf infestation in Kansas in 1959 (216) yielded less than expected and might have been damaged by this disease. On the other hand, in Indiana (51), the disease had little or no adverse effect on winter wheat in 1959, presumably because infection occurred in the spring. Theoretically (?), the lower light intensities and low moisture stress of the cool months should contribute somewhat to the tolerance of the host. The effect of yellow dwarf resulting from fall and spring infection of winter cereals should be investigated.

Workers in Iowa (41), Illinois (127), and Michigan (134) observed that the losses from yellow dwarf in oats were aggravated on soils of low fertility. Toko (unpublished) space-planted inoculated oats, wheat, and barley in the field on fertile Palouse silt loam soil at Pullman, Wash., in the spring with uninoculated checks. The inoculated plants were severely stunted, whereas checks made outstanding growth. This has been corroborated several times by the author. The extent to which high fertility can overcome the stunting effect of yellow dwarf needs further study.

Greenhouse experiments also can be misleading because daily watering of plants (167) lessens the effects of the reduced root vigor of yellow dwarf plants. Young plants infected in the early spring outdoors are subjected to cooler temperatures, higher light intensities, and less adequate water than experimentally infected plants grown in the greenhouse during the winter season. The sum of these factors usually results in greater losses in the field than would be indicated by many greenhouse experiments.

McKinney, Specht, and Stanton (149), following a widespread reddening of oats in 1949, now believed to be due in part at least to yellow dwarf (41, 51, 211, 267), discussed factors affecting chlorophyll degeneration and pigmentations. Early senility, regardless of cause, usually disrupts the pigment system. Direct, unobstructed light and cool temperatures favor anthocyanins. Abundant nitrogen acts to stabilize the plastid system, enabling oat leaves to maintain a good green color over a range of soil pH (4.9 to 7.8).

The stage of host development at which infection occurs influences symptom development in susceptible varieties. Extreme manifestations of the disease result only from infection of the annual cereals in the seedling stage. The seedlings may die as in a seedling "blight," or they may survive for a time with the third or fourth leaf emerging in a highly distorted manner. Such plants usually fail to head; if they do, the inflorescence and entire plant are diminutive, often having a dry weight of 1 or 2% of that of normal vigorous plants at maturity. Later stages of infection proportionately reduce disease development, culminating in discoloration of only the last-formed leaf (flag leaf), the mildest visible symptom of the disease in the small grains. In late infections, the virus has only a short time in which to alter the host. The influence of time of infection upon yield reduction has been demonstrated experimentally by Oswald and Houston (167), Endo (82), Endo and Brown (86). Slvhuis, *et al.* (221), and Watson and Mulligan (255, 256).

Strain differences in the BYDV are sometimes expressed by the production of qualitatively different symptoms on a given host under similar environmental conditions. In 1 study, *Bromus commutatus* was red-purple when infected by 1 strain of the yellow dwarf virus; and severely stunted and bluish-green when infected by a second strain (47).

The genotype of the host influences symptom expression, not only in categories such as symptomless carrier, tolerant, susceptible, *etc.*, but also in ways such as the nature of the discoloration. Most barleys are yellowed, but certain varieties develop a lavender to pinkish color resembling that typical of yellow dwarf symptoms in oats (6). Some even have black leaf tips (178). Some wheat varieties are not yellowed, but may be purple or red, either comparatively pure or in addition to yellowish areas (223, 255).

The variability of symptoms on the several hosts precludes the use of host as a basis for discussing symptomatology. The range of symptoms expressed by different strains of the virus on various genotypes of the many host species may be 1 reason why no serious attempt has been made to change the name from yellow dwarf to some other descriptive name. It requires some explaining, however, to convince a farmer that his oats have yellow dwarf when they are obviously reddened or purpled.

PATHOLOGICAL HISTOLOGY AND PHYSIOLOGY

Students of the pathological histology of virus-diseased plants have added materially to our understanding of these diseases. This is a remarkable achievement as they have progressed in the absence of visible structures such as germinating spores, germ types, appressoria, hyphae, haustoria, and the like. Concepts of 2 major types of tissue relationships have developed. In general, the mosaic viruses are visualized as present in the epidermis and parenchyma tissues, as well as other host tissues, making it possible to transmit many of them mechanically through the use of expressed juice rubbed over the surface of a leaf with the aid of a gentle abrasive. Many of the primary pathological effects of these viruses result from destruction of chlorophyll. In contrast, in the yellows type of virus, the virus is usually visualized as being present and essentially limited to the phloem tissues. In these diseases, the pathologic effects may largely result from impeded translocation. The discolorations in leaves commonly associated with them follow and are the result of secondary pathological processes within the plant. In addition to these differences in gross type of attack, the yellow viruses, limited largely to the phloem, are not adapted to easy mechanical transmission but usually require the services of a phloem-feeding insect such as an aphid. In virus diseases, the search for the first visible alterations of host tissue is of great importance because they indicate the probable site of primary pathogenic action (88, 89).

In barley yellow dwarf of grasses, Esau (88, 89) found degeneration of the phloem to be the primary distinguishable internal symptom. When it is mild or incipient, the phloem elements exhibit only a deeper than normal staining reaction. When the disease is severe, the sieve elements, companion cells, and phloem parenchyma undergo necrosis. There was no evidence of hyperplasia in the phloem itself such as that caused by aster yellows and curly top viruses. The BYDV does not affect the organization of the phloem tissues, but it kills the cells apparently after they have developed normally. In severe cases, the necrosis may extend to the xylem. Allen (4, 5) also found BYD primarily destructive to phloem.

Although the results of Mueller, *et al.* (155), obtained by injecting nonviruliferous aphids with different sources of virus, are capable of several interpretations, they may furnish additional evidence that the BYDV is present largely in the phloem. When they injected both apple grain and English grain aphids with haemolymph of viruliferous aphids, the rate of subsequent transmission was at least twice that obtained when crude extract of diseased plants served as the source of virus.

Before leaving the phloem in this discussion, another aspect presents itself. Esau (90) commented in her study of sugar beet yellows that mature sieve tube elements are devoid of nuclei. She went on to state that Bonner (31) has concluded that the bulk of ribonucleic acid (an important constituent of plant viruses) is synthesized by nuclei. This would require that the actual synthesis of virus ribonucleic acid takes place in cells containing nuclei. Young sieve tubes and the companion cells then should be a logical source. Mittler (152), in studying the actual rate of fluid uptake by aphids, has concluded that mature, highly functional sieve tubes must of necessity be tapped by the aphid stylets, not just "phloem" as usually reported. His conclusion is based on the calculation that an actively feeding aphid obtains fluid equivalent to the contents of as many as 100,000 cells/hour in some instances. The virus ribonucleic acid probably originates in nucleated cells, receives its protein shell in the cytoplasm, and is then distributed, probably in lesser concentration to the cytoplasm of mature sieve tubes, and eventually into the phloem stream itself.

Certain visible abnormalities in other tissues are associated with the degeneration in the phloem. Gum deposits occur in xylem of oats and barley (89), particularly in the stem. A sugary exudate forms within the intercellular spaces of the mesophyll of the blades of diseased Clinton oats. It accumulates in the substomatal cavities and exudes upon the surface of the leaf. There were no mechanical ruptures in the leaves through which this exudation occurred, such as those reported for curly top (89).

Esau's observations help to explain the thickening and stiffening of leaves of diseased cereals. She found that leaves of diseased oat and barley plants were, sometimes at least, almost twice as thick as healthy leaves. The thickness resulted occasionally from an increased number of cells in the blade, more frequently from enlarged cells. Cell walls in leaves of diseased plants may be thicker than normal.

Activity in the terminal meristem of BYD plants of wheat, oats, and barley decreases markedly (89). According to Esau, leaf initiation is delayed, the number of leaves initiated is decreased, leaf elongation is progressively retarded, and the differentiation of the inflorescence is delayed. Delayed maturity is a rather constant symptom among the cereal suscepts, as is shortening of the stem, sometimes to a degree justifying the name dwarf. This reduced meristematic activity thus contributes to the alteration of host structures.

Little is known concerning the fate of plastids and pigments within BYD plants. For example, it is not known whether the discolorations of diseased leaves result from increased xanthophylls and carotinoids, or whether their presence is revealed by degeneration of the chloroplasts. The brilliance and depth of the reds, purples, and yellows suggest an actual increase of these pigments.

McKinney, *et al.* (149) studied the pigmentation of discolored oats in free-hand sections. The anthocyanins were found mainly in epidermal cells. These anthocyanins were red, maroon, oxblood, carmine,

scarlet, and violet. In leaves in which little chlorophyll remained and the epidermal cells were nearly free of anthocyanin, deeper lying pigments were unmasked. These were carotinoids and yellow or terracotta, water-soluble pigments imparting orange, reddish orange, terracotta, and yellowish orange hues. The color changes in degenerating oat tissues are especially subtle because anthocyanins, sometimes referred to as vegetable "chameleons," vary in color (28) with changing hydrogen-ion concentration of the sap, with degree of methylation, *etc.*

Colwell (59) detected yellow dwarf in cereals by aerial photography. The diseased plants reflected significantly less infrared light than healthy ones. According to Colwell, infrared light is unaffected by chloroplasts and is reflected largely by a turgid spongy mesophyll such as that found in healthy plants. This failure to reflect infrared light would indicate a lack of turgor in the mesophyll of yellow dwarf plants.

The physiological bases for the above symptoms and pathological histology are becoming increasingly known. Starvation might cause the blasting of spikelets in oats. A similar condition can be produced by defoliation, whether by defoliation diseases (129) or by clipping (81). Starvation of spikelets could result from failure of the phloem to function or from decreased carbohydrate production due to loss of chlorophyll. In a study of physiological effects of yellow dwarf in barley, Orlob (159, 160) observed a profound influence on certain physiological processes. Respiration, catalase and peroxidase activity, reducing sugar content, and starch increased in the leaves; total nitrogen, nonsoluble nitrogen, photosynthesis, and transpiration decreased. Obviously, increased respiration, decreased photosynthesis, and impaired translocation could starve those organs dependent on translocated carbohydrates. In yellow dwarf plants, Orlob (159) found more carbohydrates (mainly starch and reducing sugars) in the leaves and less in the roots, than in healthy plants. Orlob and Arny (276) found that treating diseased oats with either gibberellic acid or 3-indoleacetic acid reduced disease severity. Watson (254) studied barley yellow dwarf in oats and wheat and also found accumulation of starch and reducing sugars in the leaves. The inability of diseased plants to fill the kernels, their greatly reduced root systems, along with the pathogenic effects of infection upon the phloem, and accumulation of starch and reducing sugars in the leaves present strong evidence that some of the major features of this disease result from starvation of host organs dependent upon translocated food.

GENERAL ASPECTS OF APHID BIOLOGY

As aphids are the only known vectors of barley yellow dwarf virus, their abundance and activities play an important role in the epidemiology of BYD. Hence, a consideration of certain aspects of aphid biology is important in monographic treatment of this disease. This section is intended to supply information only on those aspects that are pertinent to vector relationships and related phases of the insect-virus complex.

Feeding.—As insects devoid of chewing mouth parts, aphids subsist on liquid food, principally the fluid contents of the sieve tubes of the host plants. Indeed, the name aphid is apparently derived (92, p. 331) from a Greek word meaning "to draw liquids." The piercing-sucking mouth parts are admirably suited to this mode of feeding.

In the process of penetrating the host, the aphid places the tip of the rostrum or beak against the plant surface and then forces the stylet against the resisting surface by repeated back and forth motions until the cuticle and outer epidermal cell wall are penetrated. Penetration to a point mid-way into the lumen of the epidermal cell might require 20-30 seconds (32). Inside the lumen, the stylets are flexuous, bending to and fro. When they contact the next cell wall, saliva flows from the tip of the mouth parts, jelling rapidly, to form a solid sheath enclosing and supporting the stylets. Thus reinforced, they penetrate the next cell wall, probably in about 1 minute (32).

The penetration continues, either inter- or intracellularly until the mouth parts are seated in the phloem. This adaptation to tapping the food stream of the hosts is important, since the phloem is the supposed major site of the BYDV in its hosts. The penetration to the phloem is accomplished without visible damage to host cells (33). There is some evidence that pectic enzymes assist in intercellular penetrations (133). Regardless of the exact mechanism involved, it is known that grass aphids do feed in the phloem (4, 5, 33, 56, 150).

The time needed for the bulk of the aphids to find the phloem and establish satisfactory feeding relations is variously estimated from a few minutes to several hours. Sylvester (234) states that a minimum of 15 minutes usually is required for the stylets of aphids to reach the phloem. Miller (150) found that the stylets of *Macrosiphum ambrosiae* (Thomas) and *M. granarium* (Kirby) were usually not fully

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Fig. 1. Yellow dwarf is a colorful disease on most of its hosts, ranging from yellow through reds and purples. **A)** (Upper left) winter wheat nursery, Vancouver, Wash., May 7, 1955, showing yellowing resulting from a general fall and winter infection. **B)** (Upper right) most wheats express reds and purples (Requa, upper 3 leaves) with yellow dwarf, whereas some are yellowed only (Omar, lower 3 leaves). Natural infection, Vancouver, 1959. **C)** (Left center) healthy Cody oats (background) and diseased Cody oats (foreground) inoculated in the greenhouse with a virulent strain of the BYDV, both transplanted to the field at Pullman, Wash., spring, 1957. Note the tillering and color of the uninoculated checks and of the escape behind the stake. Diseased plants utilize moisture and fertility poorly. **D)** (Right center) oat leaves picked at random in the yellow dwarf nursery, Vancouver, 1959, showing the typical range of colors exhibited by the bulk of the varieties of spring oats. **E)** (Lower left) 2 spring barleys growing in the yellow dwarf nursery, Vancouver, 1959, showing the marked influence of host variety upon symptom expression. C.I. 5020 (left) turned yellow; C.I. 4369 (right) turned lavender-pink. All the commercial varieties tested to date have a typical yellow reaction. **F)** (Lower right) pressed leaves of 2 barley varieties, 1 with the typical yellow reaction, 1 with the more unusual lavender-pink.

extended until after 5 hours of feeding on the host. Watson and Nixon (258) found that most green peach aphids [*Myzus persicae* (Sulz.)] obtained little food from the potato in the first hour. The time factor is important in relation to its bearing on the speed of possible acquisition of virus from a diseased plant and its inoculation into the phloem of a healthy plant. The bulk of the studies indicate that phloem-probing requires from 15 minutes to an hour or more, but it should be kept in mind that, in grasses, many veinlets are quite near the surface and possibly could be reached in less time. Up to now, however, transmission studies with grass aphids and the BYDV support the basic observations on the time required for most individuals to attain a feeding position.

Feeding on the liquids of the phloem after penetration is accomplished requires very little effort, if the host is turgid, according to Kennedy and Stroyan (133). After certain aphids had been feeding satisfactorily upon a host, their beaks were severed without disturbing the stylets in the phloem. Juices exuded from the stumps of these severed beaks for hours, showing that the plant sap is under pressure; and, consequently, that the aphids need not apply suction to obtain nourishment. On the other hand, if the natural flow of fluids is excessive, it can be controlled by the aphid to suit itself. As a plant loses turgidity or becomes dry, this enviable situation of essentially effortless feeding is lost and the aphid must apply suction to obtain its food. The energy required to extract juices is significant in aphid movement; for when the labor becomes burdensome, the aphid becomes restless and seeks another, more palatable host. In so doing, it may carry virus to another plant.

This dependence upon a host in a good growing condition has kept the grass aphids polyphagous (133). The grasses of the temperate regions are highly inconstant hosts, progressing in their developmental stages from succulent to dry in a short time. To cope with these vegetative rhythms, the aphids shift from early to late developing hosts, when necessary for survival. By this shifting habit, they have avoided becoming dependent on a single host plant. Migrating from host to host is important in extending the natural host range of the virus and in the movement of the virus from perennial reservoir hosts to annual cereals and from 1 cereal to another.

The presence of aphids on wilted plants demonstrates their ability to apply suction. Rochow (191) employs a "cut-leaf" technique in which he feeds aphids on pieces of detached leaves of diseased plants. The aphids feed on these leaf pieces for a few days and obtain virus as well as nutriment from them. It is assumed that there is no positive pressure in such leaf pieces, although this is not certainly so, since detached stem pieces of woody species can develop local pressure (30).

Nutrition and Water Requirements.—The adaptation of aphids to a diet consisting largely of sieve tube contents has resulted in a simplified digestive system. A liquid diet has the advantage of easy acquisition. It has the disadvantage of being nutritionally unbalanced to meet the needs of the aphid. Plant sap is high in water and carbohydrates, particularly sugars (133); but low in some critical proteinaceous material and, most likely, vitamins. Whatever the nutrient in short supply, the constitution of the sap is altered as it passes through the aphid gut. When passage is copious, the aphid rejects much of the carbohydrates and water to form honeydew, thereby removing a larger proportion of the nitrogenous materals.

The concentration of proteinaceous or nitrogenous materials relative to carbohydrates within the aphid may be accomplished by differential absorption through the wall of the gut, or in some species, with the aid of a special "filter chamber" (133; 204, p. 134). If this tendency to concentrate the nitrogenous fraction of the phloem sap within its body exists to any extent in aphids, it is conceivable that by this means the virus present in plant sap is increased to a higher level in the body juices of the aphid. This could play a part in "charging" the aphid sufficiently to maintain a viruliferous condition for life from a single acquisition feeding.

Diseased plants may differ sufficiently chemically from adjacent healthy plants to affect the nutrition of various aphid species. Baker (19), studying sugar beet yellows, found that 4 species of beet aphids preferred diseased to healthy beets as food plants. In this case, the preference was not due to color changes alone; these aphids lived longer and multiplied more rapidly on the diseased plants. The superiority of diseased plants as food is probably due to an alteration of the amino acid content, rather than to changes in the carbohydrate portion of the fluids. In curly top of beets, Fife (104) found that of the several amino acids he studied, all but cystine occurred in greater concentration in the leaves of diseased beets. As yet, no studies of this nature have been

made on the yellow dwarf disease. Students who contemplate such should be mindful that color does influence the choice of plants by aphids, and that the grass aphids may not prefer yellow as is the common preference of dicot-feeding aphids, according to the trapping trials of Eastop (78) and Orlob and Medler (163).

Ross (204) emphasizes water economy as a major problem of small-bodied terrestrial animals. The body surface of aphids is large in relation to their bulk, posing problems of excessive water loss when they are not attached to a suitable host. Although the exoskeleton contains water-retaining fats, waxes, chitin, and insoluble protein, the aphid is soft-bodied and subject to desiccation. When detached from a succulent host, the life of the aphid is usually short, particularly in hot, dry air. Perhaps, poor water economy is at least partially responsible for this weakness.

Apparently different species respond to desiccation in about the same degree. Broadbent and Hollings (37) found that 5 species of aphids were killed by an exposure of 1 hour to 38-41°C in 60% relative humidity. They cited reports of whole populations of aphids being quickly reduced in number by sudden elevations in temperature. In all probability, therefore, a migration of air-borne forms could be quickly destroyed by hot, dry air. Ruggles and Wadley (206) point out, however, that the greenbug can survive several days at 50°F without feeding, partially explaining the ability of that aphid to survive prolonged aerial journeys in the spring of the year.

Reproduction.—Aphids are among the most prolific of insects. For the most part, the grass aphids exist largely as parthenogenetic females. As such, each aphid can reproduce. Few individuals of these species are wasted as males. One parthenogenetic female usually produces 10-30 nymphs, but this statement leads to an underestimation of their true reproductive abilities. According to Kennedy and Stroyan (133), the time lapse between generations is more important than the number of offspring/individual. The generations may overlap as the first-born of an individual may mature and begin reproduction while its mother is still bearing young. Kennedy and Stroyan further point out that aphids "telescope" the generations in another way in the ovoviviparae. The adult parthenogenetic female deposits the nymph, the egg having hatched just prior to its emergence from the vagina (ovovivipary). (Vivipary usually refers to hatching and a period of development of the offspring within the mother prior to parturition; ovovivipary refers to hatching of the egg within the mother just prior to parturition.) At this time, the embryo of the next generation is in the newly born nymph. In other words, the mature aphid with a developed nymph ready for birth is already a grandmother, in a manner of speaking.

Davis (73) observed that the apple grain aphid is not as prolific as the greenbug. Even so, with 30 individuals/female, the progeny of a single apple grain aphid would almost cover the land area of the earth in 15 generations. This would be enough aphids for more than 6,000/in.^{2} over all of Texas. Obviously, therefore, the aphid is capable of producing tremendous populations, and only strong adverse environmental factors prevent fulfillment of the potential indicated.

Aphids are specialized (133) for certain functions, and the rate of multiplication varies in the different forms. The wingless ovoviviparae (apterae) are the simplest, morphologically and physiologically, and reproduce the fastest. Winged ovoviviparae (alatae) are more highly differentiated; in some species, the winged forms are more restless or nervous. The oviparae (egg-laying females) are still more specialized and least fecund. These generalizations are valid for the greenbug, at least (248).

Wings.—Like animals in general, aphids possess the capacity of multiplying to the point of exhausting the food supply of any habitat (151). Walking does not provide sufficient movement for escape from intense competition of local build-ups. In serious outbreaks of the greenbug, for example, the host may collapse with such rapidity that wingless forms are left stranded to die as great numbers crawl over the soil surface in a futile search for food (131). Wings, therefore, provide a ready means of escape from intense competition of this kind, and incidentally, provide for long-range distribution of viruses of the persistent type.

Entomologists are in fair agreement that among the greatest stimuli for wing development are hunger and crowding. Comstock (60, p. 417) reports rearing 60 consecutive wingless generations in the greenhouse by moving aphids continually to fresh food plants. That these aphids had not lost their ability to form wings was proven by allowing a portion of the sixtieth generation to reproduce undisturbed. Before long, wings appeared on the aphids on the crowded plant, whereas those transferred to fresh plants remained apterous.

Factors other than crowding and food supply influence wing formation in parthenogenetic females. Ewing (95) noted that wingless apple grain aphids tended to produce more winged offspring, whereas winged females produced fewer winged offspring. Ackerman (2) confirmed this observation under most conditions. He hypothesized that wing-formation required a wing substance and that the production of wings in 1 generation tended to exhaust the supply of this substance in the aphids and lessen the amount in the succeeding generation, enabling the development of wings in the parent to influence the progeny by means other than heredity. Primordial wings are formed in the embryos of unborn aphids (136). This tendency for a winged-wingless-winged alternation, particularly strong in the greenbug (248), is important, in that if a flight of viruliferous aphids alighted on young healthy grain, its winged offspring would not be produced before the virus had become systemic in the host. Thus, the bulk of successive winged individuals would, like their predecessors, be viruliferous.

Temperature is an additional factor influencing wing formation. Ewing (95) studied apple grain aphids developing in temperatures ranging from 60° to 90°F and found that fewest winged individuals developed at 65°F. He believed this temperature prob-

ably represented the optimum for metabolic activity of tbe apple grain aphid. Ackerman (2) extended the temperature range from 12°C to 26°C and found few winged individuals at 12° and at 18-20°C, thus demonstrating 2 temperatures unfavorable for wing development in the apple grain aphid. The corn leaf aphid (53) produced no wings at 84-90°F, but at 60-70°F many winged individuals appeared. Wadley (248) found that the fluctuating outdoor temperatures of spring and fall in Minnesota stimulated wing formation in the greenbug. Day-length played no part.

Wing production also is stimulated by the approach of sexual reproduction in those aphids that use both herbaceous and woody plants (as the apple grain aphid) in their complete life cycles. The forms that leave the grass host for the apple in the fall are winged, as are the forms (parthenogenetic) that leave the apple for the grass in the spring. This type of wing formation is in response to more dependable stimulation than those stimuli found in summer ovoviviparae. It is obvious that wings appear in response to a number of diverse stimuli, but present knowledge of this subject is inadequate.

Flights.—Winged ovoviviparae of most species are encouraged to flight by moderate to light air movement. They are not blown from the plants into flight, but launch themselves voluntarily into the wind, toward the light source (133). Their tiny wings propel them horizontally at a speed of only a little over 1 mph (34, 113). If they were dependent on their own limited strength, they would not get far, even by alternately flying, resting, feeding, and flying. This type of activity would be further limited as the wing muscles undergo degeneration after a period of a few days.

To facilitate flight, the aphids launch themselves forcefully into winds of moderate velocity (up to 3-7 mph). Broadbent (34) states that prior to take-off the aphids climb to the upper parts of the plant on the windward side and test the wind, or feel it. Webster and Phillips (263) noted that the greenbug often goes down toward the base of the plant in windy weather, then at a propitious moment enters the swirling air at the soil surface and is swept away. Wind stimulates the greenbug to fly (248). Shaking the plant, especially in warm weather, acts as a mechanical stimulus to flight.

When they rise above the level of the crop plants and enter the moving mass of air, the aphids orient their bodies perpendicular to the surface of the earth, and from then on use their wings only for adjustment of elevation (133). not for forward motion. Thus, they passively ride the air currents, conserving their own strength. The bulk of the aphids are believed to seek to end their flights in a few hours, before exhaustion or desiccation weakens them below the point of survival. The aphid changes its flight position in the air at that time and actively attempts to alight. Alighting is a critical stage of flight and requires calm air.

The preference of aphids for gentle to moderate winds in which to launch flights tends to cause underestimation of probable flight distances. Air movements at the surface of the earth are more subdued than those slightly higher. Broadbent (34) reports that within a potato crop the wind may be 3 mph, but that at 2 m above it may be 15 mph. Thus, transport by such a wind for a few hours would accomplish a considerable change in position. Flights of 50-200 miles have been verified for the greenbug (248).

The mechanism of flight is well illustrated by the greenbug invasion of Minnesota and Wisconsin (10, 274, 275) in 1959. The aphids were apparently carried by "high southwesterly winds from Oklahoma, Kansas and adjacent states. The winds diminished in Minnesota and the aphids were dropped along a cold front. . . . The first and heaviest infestation occurred along this cold front; subsequent infestations probably taking place from later high winds which scattered the initial one."

The presence of aphids on scattered host plants has given the impression that they possess some sensory mechanism effective in locating suitable hosts, even at a distance. Kennedy and Stroyan (133), in their review of biology of aphids, state that, other than attraction to colors (yellow, red, green), aphids find their hosts only by random dispersals of large numbers of frenetically active migrants, most of which die in the process. Wadley (248) observed that a walking greenbug does not respond to the presence of a host plant farther than 6 mm, and it is doubtful that their eyes in flight can accomplish much selection (other than color) at any distance.

Population.—The grass-feeding aphids with which we are concerned develop their largest populations during prolonged periods of cool to moderate weather devoid of heavy, pounding rains. This is true in spite of the fact that the time from generation to generation is lengthened in cool weather (aphids are cold-blooded animals and respond directly to temperature changes within a wide range). Early American entomologists (73, 263) observed that the apple grain and English grain aphids and the greenbug were able to multiply slowly at about 40°F. Temperatures between 40-45°F and 56°F permit the aphids to multiply somewhat more rapidly, but still greatly restrict or halt the activity of the major predators and parasites (later workers have elevated the upper range advantageous to the aphid to about 60-65°F). Thus, in the lower temperature ranges permitting reproduction, the aphids have a relative advantage over their biological enemies. Even though the corn leaf aphid is adapted to a slightly higher temperature range, Wildermuth and Walter (266) state that they also reach their greatest numbers in relatively cool weather.

According to Walton (251), a definite sequence of conditions usually precedes astronomic populations of the greenbug. For example, the preceding summer was relatively cool and wet. Grain that shattered or lodged and came in contact with the soil germinated and made heavy growth in the summer and early fall and was infested by aphids. The aphids multiplied rapidly in this volunteer grain and also in early-seeded, rank fall-sown grain. The ensuing winter was mild, with extensive survival of ovoviviparae (parthenogenetic females), and the spring was prolonged, cool, and delayed. Under these conditions, an essentially uninterrupted multiplication took place over a

long period. Along with this sequence of conditions, predators and parasites were scarce. In his account of a southwestern (Oklahoma, Kansas) rampage of greenbug, Kelly (131) laments that although the grain was dying in April, there still were essentially no predators. By May 15, the farmers were plowing out their spring oats as a total loss.

The ability of grass aphids to multiply at temperatures lower than their known major enemies is of significance for another reason. The small grains (oats, barley, wheat, rye) are normally in a juvenile state during the cooler portions of the growing season, whether fall- or spring-seeded. It is well known that the earlier infection occurs in cereals, the more detrimental the disease becomes (86, 87, 167, 221, 254). Thus, the BYDV aphid vectors as a group are well suited to develop and disperse at the time of the year when the host is in the stages most susceptible to the BYDV.

Predators.—A predator on insects is another insect that destroys its prey by devouring it directly, as a lion eats a sheep. The most efficient predator of these grass aphids is usually the convergent lady beetle (*Hippodamia convergens* Guer.) (Fig. 2). Fenton and Fisher (102) observed that this beetle was active earlier in the spring than "parasitic" species, and therefore of greater value as an enemy of the greenbug. Wildermuth and Walter (266) found that the convergent lady beetle and *Ceratomegilla fuscilibris* Muls. were the most important predators of the corn leaf aphid (they list many predaceous species). Each lady beetle larva can consume 30-100 aphids daily (126).

Birds, lizards, and other forms of life are listed as often feasting upon the aphid. When winter barley became heavily infested with the corn leaf aphid, Wildermuth and Walter (266) recommended grazing it with cattle. In eating the leaf whorls, the cattle ate most of the aphids.

Parasites.—Parasites differ from predators in their *modus operandi*. The insidious manner in which the most widely acclaimed parasite of the BYD aphid vectors, a tiny wasp [*Aphidius testaceipes* (Cresson)], attacks its hosts, was described by Webster and Phillips (263) and Dunn (77). The wasp most frequently thrusts its ovipositer into the abdomen of wingless ovoviviparae that are about half grown (Fig. 3). The egg of the parasite hatches within the host, developing into a larva that gradually destroys the aphid. If the aphid is not yet in the third instar when parasitized, it usually dies without reproducing. A more advanced victim usually reproduces until the larva within it attains its third instar. The fourth larval stage of the parasite is active and it turns about within the aphid, devouring the internal organs of the host. By this time, the aphid shows obvious signs of parasitism. It is darker and shiny. The parasite fastens it to the leaf with a few wisps of the material it uses to build its cocoon. The cocoon is spun within the empty carcass. At this time, the parasitized aphid is a brown or black mummy—dry, swollen, and distorted—with parchment-like skin adhering to the host plant. When the wasp is mature, it emerges through a round hole it cuts near the cornicles. The parasite may overwinter in these cocoons within the exoskeleton of the aphid.

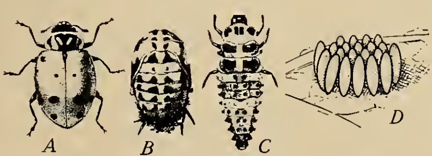

Fig. 2. The convergent lady beetle (*Hippodamia convergens* Guer.) (from U.S. Dept. Agr. Circ. 346, 1935), a major predator on aphids. **A)** Adult beetle; **B)** pupa; **C)** mature larva; **D)** egg cluster. The adult, pupa, and larvae are orange and black and about ×4 natural size; the eggs, lemon yellow and about ×8 natural size.

Fig. 3. The female of the parasitic wasp [*Aphidius testaceipes* (Cresson)], depositing an egg in a greenbug (by Webster, from Webster and Phillips, 263).

The aphid has a wider wing span and is better adapted to ride the wind than the heavier wasp (126). The relatively heavy-bodied adult wasp is largely dependent on its own wings for propulsion. Thus, this parasite depends upon the egg or very young larva within a still active migratory host for long range dissemination. The wide distribution of the parasites is readily understood when you consider that an aphid, mature or well developed when parasitized, can fly with the migration bringing its enemy to the new location within itself.

Hunter (126) and Glenn (112) point out that migrating aphids in early spring may be free of the parasite because cold temperature limits the parasite more than the host. The adult wasp is immobilized by 35-36°F and killed by 17°F. It can move lethargically and manages to sting (oviposit) a few greenbugs at 38-40°F, but does not attain normal activity below 70°F. At 55°F or below, the parasite multiplies slowly, requiring a month to mature at that temperature. At 35°F, the developmental stages within the aphid mummy require 114-140 days, thus explaining its method of overwintering.

Parasites of this type have been important in reducing populations of the greenbug (126. 252), apple grain aphid (73), bird-cherry oat aphid (77), corn leaf aphid (266) and the English grain aphid (128. 252). They are not limited to a single species of aphid, and presumably they attack most of the species present at any given time (77). The parasitic wasp is usually the major insect enemy of the greenbug in the southwest (North Texas, Oklahoma, Kansas), while ladybird beetles are its major enemy in the north (Minnesota) according to Wadley (248).

In spite of the undoubted importance of predators and parasites in nature's scheme, they have often developed too late to control aphid outbreaks in the large grain area of Midwestern America. Parasites and predators are most effective in equable climates (225) where host species are more or less constantly present, providing food for and preventing the enemy species from sinking to exceedingly low levels. In areas with severe climates, a "lag" between parasitic and predaceous insects and hosts is almost inevitable. The former cannot multiply substantially until the prey is abundant, and thus the parasite begins to accelerate at a time when the aphid is already going strong. As the predaceous and parasitic insects are not limited to a single host species, Marcovitch (145) pointed out the value of mixed vegetation in providing food for more host species in a greater portion of the year, thus maintaining the aphid insect enemies at a higher year-round level. Lady beetles can augment their diet with pollen, molds, and other insects.

Parasitic Fungi.—There is little evidence to support the view that entomophthorous fungi are important enemies of the grass aphids. Although Phillips (179) reported that a mold became rampant in his cultures of English grain aphids under warm humid conditions, the fact that most workers have not experienced such occurrences is probably more significant. Harris (116) studied *Entomophthora coronata* (Cost.) Kevorkian, which attacks potato aphids in Maine. The fungus was pathogenic on aphids but did not become destructive to them until they were numerous. Hall and Dunn (114) in California reported that several *Entomophthora* spp. were important enemies of the alfalfa aphid. MacLeod (143) found *Empusa* (*Entomophthora*) spp. on several insects throughout Canada.

It appears that in most observations the biological enemies of aphids (predators, parasites, molds) become most effective after the aphid has reached abundance. This would be too late to save that area from yellow dwarf: a small, well-distributed population is all that is needed for vection. The biological enemies, however, could destroy or greatly reduce a major aphid population in an area and in so doing limit the size of flights from such an infested area. In temperate climates, biological enemies (parasites, predators, molds) are less important in governing aphid populations than are the physical factors of the environment. Physical factors, such as seasonal temperatures and distribution of precipitation, not only influence the aphid directly, but also by setting the portions of the year when food plants can grow. A brief review of some physical factors follows.

Rains.—Aphids, like all forms of life, are subject to destruction by weather violence. They are soft bodied and subject to direct physical damage. Heavy, driving rains dislodge them from exposed plant surfaces and beat many of them into the soil. They have difficulty in walking on wet soil surfaces and might be unable to climb back up the plant (34). The greenbug is especially susceptible to damage by driving rains. Fenton and Fisher (102) observed destruction of a heavy infestation near Stillwater, Okla., by a single shower of 20 minutes duration while the aphids in the surrounding areas were undamaged by greater total precipitation that fell gently. Frequent. heavy rains when temperatures were favorable to the greenbug were regarded by Wadley (248) as the reason for the comparative unimportance of the greenbug east of Oklahoma.

Low Temperatures.—The ovoviviparae of each species are killed by temperatures below certain critical levels, but little agreement can be found in the literature on this point. Possibly the degree of hardening, both of the insect and host plant, and the thickness of the vegetative cover are factors varying the lower limits of cold tolerance. A second type of death from cold, gradual disappearance, is important. The statement that the corn leaf aphid gradually disappears during the winter (72) leads to the belief that aphids overwintering as ovoviviparae, even though well-hardened, nevertheless disappear because they do not reproduce fast enough to replace those that die during the cold season. In this way, unless the weather is occasionally warm enough to permit birth of young during the winter, the population gradually disappears. Greenbug "disappearance" of this type was described by Wadley (248).

Drought.—None of the BYDV grass aphids has a "dormant" state in which to endure periods of extreme drought. Their populations are essentially annihilated in an absence of succulent food in warm weather. In parched summer areas of California (235), the English grain and apple grain aphids have resorted to such hosts as the cat-tail rush (*Typha* sp.) and the California tule (*Scirpus* sp.). The apple grain aphid also was found on the dragon tree (*Dracaena draco*) and banana (*Musa sapientum*). Davis (73) had previously listed *Typha* as a host.

VECTORS

The BYDV is obligately vector-transmitted. At least up to now, all efforts to transmit this virus by other means (seed 167, 184, 238, 267; soil 167, 238; and manually 46, 49, 167, 238, 267) have failed. It must be transmitted by aphid vectors, of which there are at least 9 species. Oswald and Houston (167) discovered 5 aphid vectors: the apple grain aphid, *Rhopalosiphum fitchii* (Sanderson): the English grain aphid, *Macrosiphum granarium* (Kirby); the corn leaf aphid. *Rhopalosiphum maidis* (Fitch); the rose grass aphid, *Macrosiphum dirhodum* (Walker); and the greenbug, *Toxoptera graminum* (Rondani). (Oswald and Houston (167) listed the apple grain aphid as *R. prunifoliae* (Fitch), but the presently accepted binomial in the United States for the apple grain aphid is *R. fitchii.*) Orlob (159) added the vector *Rhopalosiphum poae* (Gillette) to this list in Wisconsin and European workers added the bird-cherry oat aphid *Rhopalosiphum padi* (Linnaeus) (184, 259, 268), *Sitobium fragariae* (Walker), and the crescent-marked lily aphid *Myzus circumflexus* Buckton (259). Butler, *et al.* (49) in New South Wales, Australia, found *Macrosiphum granarium* s.-sp. *miscanthi* Takahashi as a vector. Possibly other vectors also exist, but those already known show that this virus has the advantage of being transmissible by an adequate range of species.

Efforts to transmit the BYDV with certain other species have so far failed. Orlob and Medler (163) failed with *Myzus persicae* (Sulz.), *Sipha agropyrella* Lambers, and *Hysteroneura setariae* (Thom.). Slykhuis, *et al.* (221) were unsuccessful with *Sipha* sp. and *Rungsia* sp. found on diseased barley. *Sipha agropyrella* from diseased wheat and barley in Washington did not transmit the virus. The existence of vector-specific strains of the BYDV, however, might explain some of the negative results.

All vector species are not equally effective in transmitting the BYDV. The various species of aphids differ not only morphologically, but also in more subtle physiological and behavioral ways which influence their effectiveness as vectors. They differ in their abilities to transmit given strains of the BYDV, in their preference for different grasses, in their rate of multiplication under different temperatures, in their feeding and flight habits, and in overwintering abilities.

The life cycles of the major vectors of the BYDV also differ, as shown in the brief descriptions that follow.

THE ENGLISH GRAIN APHID.—*Macrosiphum granarium* (Kirby).—The English grain aphid is 1 of the most widespread aphids of America, Great Britain, continental Europe, and Japan (224). William Kirby described this aphid in 1798 as *Aphis granaria* Kirby. He thought that this species might be the same as that of Fabricius, *A. avenae* F. The species was transferred to *Macrosiphum* by Schouteden in 1901. (Note that in entomological nomenclature the first person adequately describing a species is the only author of the species: those subsequently shifting it from genus to genus are not listed after the species. Another feature of entomological nomenclature is that parentheses about the author's name indicates that it has been removed from the genus in which it was originally placed.)

The author was confused to find some authors referring to the English grain aphid as *Macrosiphum avenae* (F.) or as *Sitobium avenae* (F.). Miriam Palmer (personal correspondence) explained that Fabricius (1794. Ent. Sept. vol. 4: 214) described *Aphis avenae* F. as an aphid from oats with a white cauda. Some European authorities consider this aphid to be the English grain aphid, but other aphids commonly found on oats fall within the sketchy description given by Fabricius. The description of Kirby was sufficient to lead Theobald (Aphididae of Great Britain, vol. 1: 74) to state, "There is no doubt of it (the English grain aphid) being Kirby's species, (*granarium*) though the description is meager." Palmer concluded that the surer ground is to hold to the name of *Macrosiphum granarium* (Kirby). It is a major vector of the BYDV (49, 119, 153, 161, 167, 169, 197, 221, 230, 238, 250, 257). Butler, *et al.* (49) in New South Wales found *M. granarium* s.-sp. *miscanthi* Takahashi a vector.

The English grain aphid spends its entire life on the Gramineae. In regions of mild to moderate winters, it may spend the year as parthenogenetic ovoviviparae (virginiparae) on grasses. It may exist the year around in this way in Illinois (123), Indiana, Virginia (179), and west of the Cascade Mountains in Washington (43). Phillips (179) believes that north of Indiana the insect can overwinter as eggs or ovoviviparae or both, depending somewhat on the season. He doubts the egg stage occurs at all south of 35°N latitude in the United States, except possibly at high elevations.

The common form of the aphid usually observed feeding in grains and grasses, the "summer" ovovivipara, is green to yellowish green with prominent dark cornicles and dark-tipped legs. They are not gregarious when feeding on young grain, but usually are scattered sparsely over the plant surface as solitary individuals or in small clusters. Summers and Bowman (230), in Mississippi, observed the tendency of this species of aphid to spread widely as opposed to the greenbug (*Toxoptera graminum*), which usually develops in spots until competition forces dispersal. The tendency to disperse uniformly, rather than to develop heavy local populations, would increase the efficiency of a given population as vectors.

When the grain begins to head (105), the aphids, as if by signal, leave their feeding positions on vegetative portions of the plant and assemble in the inflorescence. This preference for the juices involved in kernel formation is so strong that they crowd together on the inflorescence in congested masses. At this time, many of them undergo a change in color, becoming orangish or yellowish pink. Color changes occur also (179) in the fall, just prior to the appearance of sexual forms. As the grain ripens, the aphids move to the more succulent late summer and fall grasses.

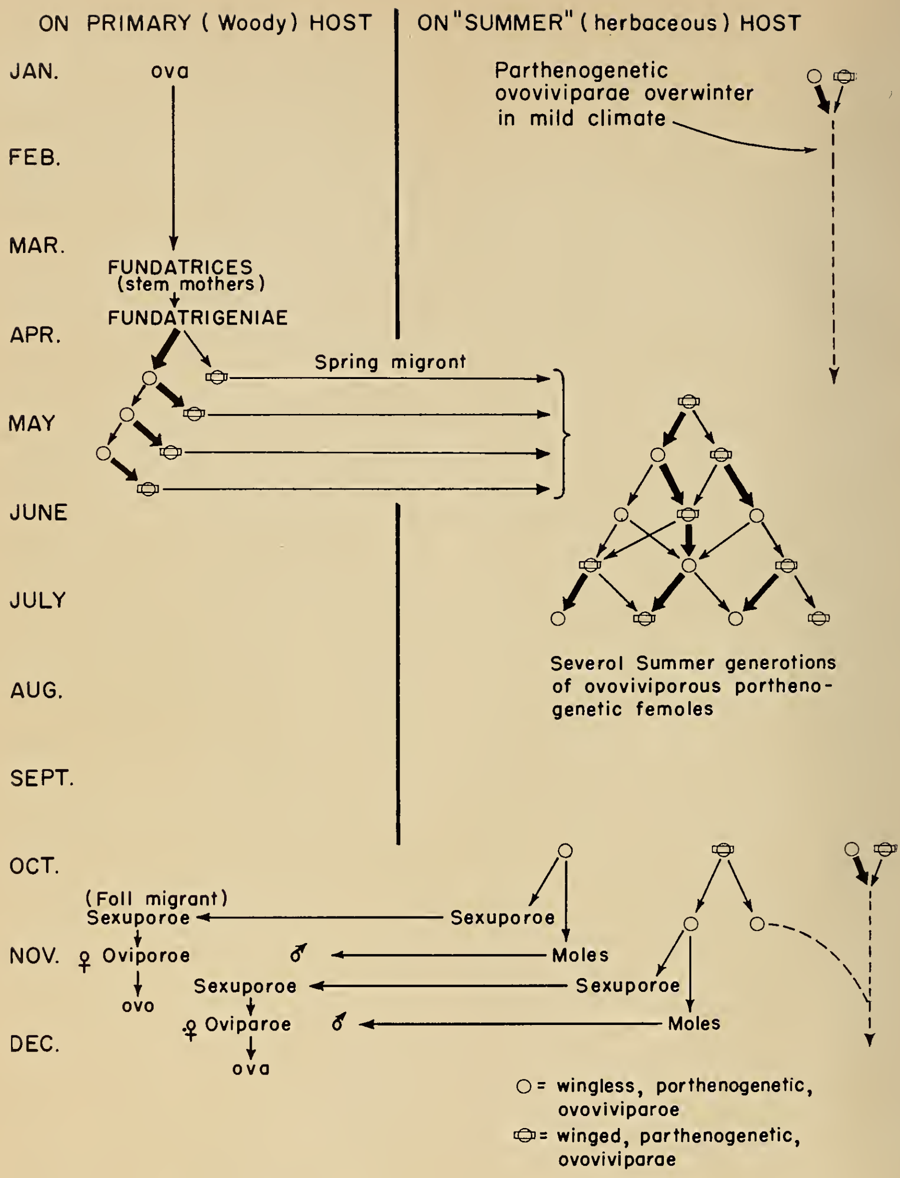

Fig. 4. Diagrammatic life cycle of the apple grain aphid (*Rhopalosiphum fitchii*), showing stages spent on the primary host (probably apple or hawthorne) and on the secondary host (grasses). The spring migration from the primary to the secondary host may be abrupt (completed in 2 generations) or prolonged (up to 4 generations). The appearance of the fall migrants and males is usually scattered over considerable time also. Note particularly that the aphid may propagate continuously as parthenogenetic ovoviviparae in climates of mild winters.

According to Phillips (179), the typical green aphids in the fall are parthenogenetic ovoviviparae and the pink forms give birth to light pink or dark pink nymphs. The light pink nymphs, when mature, give birth to winged ovoviviparous sexuparae that become mothers of wingless, yellow oviparae (the true females that require fertilization for the formation of fertile eggs). The deep pink nymphs develop directly into males. Phillips (179) also observed that the oviparae laid only an average of about 8 eggs/female, and these either did not hatch or the number hatching was very low. The eggs, which are deposited on grass blades in November, are elliptical, 0.3 x 0.7 mm, pale yellow changing to green, then to black. They hatch in late March and early April (179, 224). In 1908, only small percentages of the eggs hatched. If this is typical, apparently the aphid in the egg stage can overwinter only in small numbers. Also, if eggs were the only source of the species in the spring, the population would increase so slowly as to preclude the possibility of an epidemic of yellow dwarf in spring grains, except possibly in years of late crops.

The Apple Grain Aphid.—*Rhopalosiphum fitchii* (Sanderson).—The apple grain aphid, unlike the English grain aphid, uses both woody and herbaceous plants in the complete life cycle (Fig. 4). In cold regions, sexual forms develop and the aphid may overwinter in the egg stage upon apple (*Malus* spp.), hawthorn (*Crataegus* L.), pear (*Pyrus* L.), quince (*Cydonia* L.), mountain ash (*Sorbus* sp.), ninebark (*Physocarpus opulifolius* (L.) Maxim.), *Mespilus* spp., and *Cornus* sp. The subfamily Pomoideae of the Rosaceae is favored, with the apple or hawthorn being the most common host upon which sexual reproduction takes place (primary hosts) in the United States (18, 123, 139, 163, 177). Other woody hosts (71) are sometimes used, but they are of lesser importance. Sanderson described this aphid from forms found on apple (*Malus sylvestris* Mill.) in 1902. It is a major vector of the BYDV (162, 163, 192, 245).

The egg stage is of variable importance in perpetuation of the species in different parts of the United States, depending on the climate and the abundance of primary hosts. Ewing (95) noted that the apple grain aphid was prevalent on the Pacific Coast and that it reproduced all winter long on winter wheat at Corvallis, Ore. Lathrop (139) found that the apple grain aphid overwintered in profusion on apple in New York. In the Willamette Valley in Oregon, however, it was rare in orchards and abundant on grasses and winter cereals. A similar situation is common in western Washington (43); but, east of the Cascade Mountains in the same state where the climate is more severe, the egg stage may be significant in some seasons (personal communication from C. A. Johansen).

Baker and Turner (18) found the initiation of sexual reproduction quite complex. The fall forms on the grass host are all produced by wingless ovoviviparae (parthenogenetic females). One mother may give birth either to winged (alate) migrants (those that later give birth to the true females on the apple) and males, or to wingless ovoviviparae and males. The males are always the last progeny of that particular mother. They are winged and they fly to the apple within a few days of maturity. The fall migrants (female sexuparae) also fly to apple trees where they give birth to 4-8 true females (oviparae) requiring fertilization and capable of depositing eggs.

The oviparae mature slowly, requiring 16-20 days. The migration of males and sexuparae to the apple takes place gradually. Males that develop first arrive on the apple before the oviparae are mature. They wander about, feeding occasionally, waiting maturation of the females. Mating (18) on the apple requires but 10-15 minutes. Once a mating is accomplished the male hurries off in search of another female. The same female may be visited more than once by the males. The females can mature their eggs only when fed a diet of old, mature leaves. Succulent apple leaves do not contain the requisite foods.

Once mating is completed and oviposition begins, the females begin wandering about in search of roughened spots or crevices in the bark. Each female deposits about 2-7 eggs, laid alone. When several eggs appear side by side packed in a particular crevice, it indicates that several different females were attracted to the same spot (18). Baker and Turner found the eggs most abundant between fruit buds on the fruit spurs and in scars, usually on the smaller lower branches but occasionally over all the tree. Fitch (105) noted that many eggs may be blown or washed off the tree during the winter.

The embryo is protected by an egg shell of 3 layers (177). The outer layer is soft and glutinous when the egg is laid, becoming semitransparent and brittle. The middle layer is elastic and pigmented, becoming black. The inner layer is thin and transparent. The nymph at birth ruptures the outermost layer first, then the elastic middle layer, and finally the thin inner layer. This hatching process takes 2-8 days, depending on the temperature. Peterson (177) found that the black eggs are quite resistant to environmental changes until hatching time approaches. They then become more susceptible to changes in the environment. In New Jersey, usually about 50% of the eggs are viable in nature. In Peterson's experiments conducted at 80°F, however, only 0-4% hatched in dry air, 0-12% at 22% relative humidity, 20% at 63% humidity, and 36-46% in saturated air. The eggs are quite susceptible to lime-sulphur, which in Peterson's tests, killed 85-100% of them.

Baker and Turner noted hatching mainly between March 15 and April 10 at Arlington Farm, Va. (18). They observed that eggs sometimes hatch at any time during the winter after a few warm days. The first born were killed by frost. (They may not be as hardy as the nymphs of ovoviviparae on grasses in the fall and winter, or possibly the buds had not opened and there was no food.) It is usually cool at this time of the year, but the stem mothers or fundatrices (the forms hatching from the winter eggs) were mature in about 13 days and lived a total of 23-49 days in Virginia (18). This first generation extended from April 3 to May 26. The apple buds opened on April 4, providing food. Lathrop (139) observed hatching at Geneva, N. Y., beginning April 22 and proceeding rapidly.

The stem mothers (18) were more prolific than

ordinary summer ovoviviparae, averaging about 99 offspring each. The apple grain aphid commonly feeds in little groups on the underside of the apple leaves. Up to 4 generations can be produced on this host and they can become very numerous. A migration of winged forms begins with the first generation on apple, and sometimes the entire second generation is winged and flies to the grasses (139). It is obvious that in some areas the apple could serve as a source of sizeable numbers of apple grain aphids in the spring. But, presumably, they are nonviruliferous when they leave the apple; and, by the time they have acquired virus and multiplied sufficiently to invade cereal fields in quantity, it is doubtful that they constitute a major threat.

The transition from the woody primary host to the grass secondary host apparently requires a delicate transition within the aphid. Webster (261, 262) attempted to colonize wheat with the aphids from apple. After several failures, he finally had success sufficient to sweep away all doubts as to the existence of this migration. The same aphid from quince also colonized wheat. Orlob and Arny (162) and Richards (189) took forms from hawthorn to grain.

On grain or grass, the apple grain aphid is small, reddish brown to dusky green, and often with orangish blotches around the base of the cornicles. The color varies, with the temperature under which they are grown (2), from predominantly brown at 16°C or less to almost solid green at 29°C, near the upper limit for the species. The apple grain aphid is typically "pear-shaped" with the mid- to posterior-portion of the abdomen of greater girth than the head or thorax. Davis (73) rated the apple grain aphid as the most common and widely distributed aphid on wheat and second in importance on that host to the greenbug. It relishes oats, barley, and rye as well. It is prevalent (18) in the United States north of about 32°N.

The habit of feeding near the ground aids this species in overwintering as ovoviviparae. Cyrus Thomas (in 73) observed that overwintering ovoviviparae moved downward on grass, some even feeding on roots, in Illinois in 1879. He found well-formed nymphs below the snow. Similarly, Webster (262), in Ohio in 1893, reported that the apple grain aphid successfully overwintered in that state in mild winters without the assistance of the egg stage. The overwintering forms retreated downward to just below the ground and produced no wings. With warm weather, they moved up the plant and a portion became winged. Others have observed this use of the insulation of plant cover by this aphid (73, 173). Davis (73) noted that the rank growth of volunteer winter wheat near manure piles and straw stacks is important to overwintering ovoviviparae.

The apple grain aphid is adapted to relatively low temperatures, appearing earlier than the other major vectors in the California epidemic (168). It multiples, to some extent at least, at temperatures from 40-56°F (73). Thus, with its ability to multiply early in the spring and to carry virus to spring grains during their youngest, most susceptible stages, this aphid is of real importance to BYD. It is fairly prolific (18), with an average of 13.5 nymphs/adult on oats, with 12-16 generations/growing season.

Baker and Turner (18) observed the summer ovoviviparae on oats and wheat. The wingless mothers moved about frequently, depositing a few young here and there. For example, 1 mother left young on 4 different plants within 48 hours. The young tend to stay and develop where they were born. This tendency of the mothers to spread their young about would certainly facilitate spread of the virus from plant to plant. From their observations, Baker and Turner (18) concluded that winged aphids are no more restless than apterae.

The egg of the parthenogenetic female hatches just before it passes out of the vagina, so that the young are deposited "alive" (ovoviviparous) rather than as unhatched eggs (oviparous). The young of aphids hatch in a rather advanced degree of morphological development but are smaller than adults. They undergo simple metamorphosis, and are known as nymphs (rather than larvae or pupae which occur in forms with complex metamorphosis). The insect sheds (casts, molts) its cuticula 4 times before reaching maturity. The stage from the egg to the first molting (ecdysis) is called the first nymphal instar and the duration of this period is the first stadium. From the first molt to the second molt is the second stadium, and the insect is spoken of as the second instar.

Ackerman (2) observed that the instars of the apple grain aphid differed in ways other than in size. For example, the antennae had 4 segments at birth, 5 segments during the second instar, 6 segments during the third instar, and 6 segments during the fourth instar and in the adult stage. The fourth instar had no cauda, although the adult had a well-developed cauda. Thus, most of the instars could be identified without observing their passage from 1 molt to another from birth.

Coons (62) studied the effect of nutrition (NPK) on young oats (Garry) in nutrient solutions in the greenhouse on reproduction by the apple grain aphid. Plants receiving NPK and NP averaged 43 aphids/plant; those receiving only NK or N, 35-39 aphids; those receiving P, only 20 aphids; and those receiving PK, K, P (no N) only 15 aphids/plant. These results indicate that nitrogen plus phosphorus, and nitrogen alone are of paramount importance in the nutrition of this aphid.

The name *Rhopalosiphum fitchii* (Sanderson) may soon be replaced as the correct name of the apple grain aphid according to Louise M. Russell (in correspondence) and Rogerson (202). *R. insertum* (Walker) is an older name for this species. Probably, *R. oxyacanthae* (Schrank), still older, is a name applied to the same species. As yet, the Entomological Society of America recognizes *R. fitchii* as the correct name of the apple grain aphid.

The Bird-Cherry Oat Aphid.—*Rhopalosiphum padi* (Linnaeus).—The bird-cherry oat aphid (*Rhopalosiphum padi*) was described by Linnaeus in 1767, based on forms found on *Prunus padus* L., the European bird-cherry. It is similar to the apple grain aphid in life history, using Rosaceae as its primary

hosts and Gramineae as secondary hosts. It prefers to lay its eggs on *Prunus padus* L., *P. virginiana* L., the choke cherry, and on *P. persicae* (201). *R. padi* is so like *R. fitchii* that no detailed life history is presented. It is an important vector of the BYDV (49, 119, 127, 184, 199, 221, 223, 255, 268). It is common in England and western Europe. Its distribution and importance in America are unknown, because it has undoubtedly been frequently confused with the apple grain aphid. The 2 are so alike that no attempt will be made to detail differences [see Palmer (174) or Richards (189)].

Rademacher and Schwarz (184) found that in Germany *R. padi* left the bird-cherry late in spring and that ovoviviparae had already performed most spreading of the BYDV. Slykhuis, *et al.* (222) found in Canada that *R. padi* leaving *Prunus padus* were nonviruliferous.

The Plum Grain Aphid.—*Rhopalosiphum prunifoliae* (Fitch).—The plum grain aphid (*Rhopalosiphum prunifoliae*) was described by Fitch (105) in 1855 from forms collected on *Prunus* spp. and on apple (*Malus* sp.) in New York. According to Rogerson (201, 202), this species as described contained a mixture of the apple grain aphid (*R. fitchii*) and the bird-cherry oat aphid (*R. padi*). Hille Ris Lambers (121) considers it a synonym of *R. padi.* Palmer (174), on the other hand, maintains that there are 3 distinct species in this important fruit grain aphid complex. As the taxonomy of this group of very similar aphids is in a state of confusion at present, the author took the safest course of following Palmer. By listing the aphids as they have been identified and reported by various workers, no precision will be lost, regardless of the final outcome of the taxonomic controversy. *R. prunifoliae* is listed as a vector of the BYDV by several authors (153, 167, 169, 238, 267), but most of these reports are probably based on the apple grain aphid.

Pathologists should be certain to submit all aphids of this type used in experiments to aphid specialists for identification. This group taxes the abilities of the specialists. To make matters worse, some of the points of distinction are dependent upon differences observed among sexual forms (174), seldom used by pathologists and not even occurring in much of the United States.

The concept of the apple grain aphid (*R. fitchii*) of Hille Ris Lambers (121) is so different from that of most American workers that it was not presented.

The Greenbug or Spring Grain Aphid.—*Toxoptera graminum* (Rondani).—The greenbug was described in 1852 as *Aphis graminum* Rondani in Italy and redescribed and transferred to *Toxoptera* by Koch in 1863 (252). It is a light green aphid with a darker green stripe down its back, dusky antennae, dark feet, and dark tips on the cornicles. It leaves necrotic feeding spots on its host. Unlike the English grain aphid, this aphid does not change color markedly. It is the most directly destructive (without virus) aphid on small grains in the United States. It owes much of its destructiveness to its ability to develop under cool conditions when the hosts are small, to its unusual fecundity, to its reluctance to disperse, and to a toxic constituent of its salivary secretions. A heavy infestation of greenbug can kill young oats, wheat, or barley in less time than the incubation period of yellow dwarf. Periodically, it has devastated large areas in Texas and Oklahoma. In occasional seasons, it has been highly destructive in areas farther north.

Wadley (247) observed that the English grain aphid and apple grain aphid could live in large numbers on a given plant for weeks at a time without producing much visible harmful effect, but that an equal number of greenbugs would kill a plant quickly. Where a greenbug had fed, a faint paleness appeared within 10 hours at 26°C, or 58 hours at 14°C. The pale spot became yellow on oats and white on wheat, and was slightly longer than broad (about 2 mm long). The spot did not enlarge and damage was proportional to the aphid population. Wadley found that extracts of this aphid decolorized chlorophyll; those of the English grain and apple grain aphid had no effect. Whether the presence of this toxic property lessens the effectiveness of this aphid as a vector of the yellow dwarf virus is not known. Carter (54) noted that toxicogenic insects are seldom efficient vectors.

The effectiveness of the greenbug as a vector of the BYDV is in need of thorough study. This aphid migrated extensively in 1890, 1907, 1949, and 1959, years in which BYD is believed to have been extensively distributed in oats in much of the United States. The coexistence of the greenbug with areas suffering severe losses from BYD in 1959 (52, 119, 127, 161, 217, 241) is strong evidence that it serves as a major vector. It has transmitted the BYDV in numerous experiments (127, 161, 167, 197, 230, 238, 250). Rochow (197), on the other hand, has conducted the most extensive study to date on the abilities of the English grain, apple grain, corn leaf, and the greenbug aphids to transmit this virus. In his studies, the greenbug was the least efficient vector.

Rochow (198, 278) reported more recently, however, that different collections of greenbugs differ markedly in their abilities to transmit given strains of the BYDV. Using a strain of the BYDV from Illinois, greenbugs from Florida transmitted virus to 0 of 44 plants; greenbugs from Wisconsin transmitted it to 15 of 27 plants; and Illinois greenbugs transmitted it to 23 of 42. It is evident that considerable caution is needed in discussing, in general terms, the relative merits of species of aphids as vectors. In addition to its ability to transmit the BYDV, there is another reason for treating this aphid here. Because of its destructiveness and periodic appearance in multitudes, its population dynamics have been studied thoroughly.

Kelly (131), in 1917, stated that in the Southwest (North Texas, Oklahoma) a cool, wet summer with much volunteer grain in late summer and early fall, a mild winter, early spring a little warmer than normal, and late spring cooler than normal preceded each of the very destructive greenbug epidemics. This sequence provides a large number of aphids to enter fall-seeded grain fields, their survival in large numbers as ovoviviparae, and a spring providing the maxi-

mum duration of temperatures warm enough for aphid reproduction but cool enough to prevent effective action by predators and parasites (73, 112, 126, 248, 263). Under these conditions, the grain was often dead or dying before any appreciable number of natural enemies was present.

The greenbug seems less of a "roamer" than the other grass aphids treated here. Hence, in most seasons, it might be less of a factor as a vector of the BYDV. When feeding on a young, succulent, preferred host, it seems to start from a given source and multiply extensively in a relatively small spot before extensive movement is undertaken. Aerial photos of grain fields in Oklahoma in early stages of infestation, taken by Whitehead and Fenton (265), show many chlorotic, heavily infested spots. The apple grain, English grain, and rose grass aphids, according to the author's observations in Washington, at least, distribute themselves more uniformly, even when under no population pressure. Wadley (247) states that the apple grain aphid is the greatest "vagabond," moving about most and becoming winged with the least stimulation. The English grain aphid is quite close to it in this respect; the greenbug is least likely to shift.

Real movement and migration of the greenbug begins after it has multiplied extensively in a locality and the host is declining, forcing migration. The decline of heavily infested young grain can be so rapid that wingless and young forms die in the field (131), unable to walk the distance to fresh hosts. Migrations in Kansas and Oklahoma in which millions of aphids were in the air all day long, especially in late afternoon, were described by Kelly (131). They moved as the wind moved, irritated the eyes, and dimmed the lamp light in the streets. These heavy movements were observed in May. By this time, parasites normally are highly active, and many of the migrating aphids carried within their bodies the eggs or developing larvae of the parasite, carrying them in this manner to the new site (they were departing mainly from destroyed spring oats). Soon, they were overcome by natural enemies and were difficult to find.

Timing is important in parasite activity. Fenton and Fisher (102) noted that the major parasite, a braconid wasp (*Aphidius testaceipes* Cresson), by April 13, 1939, had parasitized 10%; and by early May, 60-70% of the aphids observed. They believed that this parasite was ineffective in this season as susceptible small grain hosts were destroyed before the parasite materially reduced the numbers of aphids. The convergent lady bettle (*Hippodamia convergens* Guer.) was of more value in this particular plague since it was present in significant numbers at a somewhat earlier date. They counted 38 larvae and 26 adults of this lady beetle/3 ft of cereal row on April 7.

The life cycle of the greenbug is similar to that of the English grain aphid in that it lays eggs on grasses in the fall, or overwinters as ovoviviparae in milder climates. Kelly (131) states that eggs of this aphid are rare south of 35°N, but that north of that line the aphid overwinters either as ovoviviparae or eggs. He observed ovoviviparae that had survived −9°F. Rank volunteer grain provides the greatest protection. For this reason, Walton (251) recommends destruction of volunteer grain on a community basis in late summer and early fall.

Minnesota is too far north for the egg stage of the greenbug to have much significance (248). Sexual differentiation is stimulated by the shortening days of September in this species. In Minnesota, the fall is cool and elongates the 2 generations needed to go from undifferentiated ovoviviparae to mature sexuals; thus, most are destroyed before eggs are laid. When eggs are laid, very few survive in Minnesota. The greenbug may overwinter effectively in the egg stage in Illinois (123), Indiana, or Virginia (263).

The Corn Leaf Aphid.—*Rhopalosiphum maidis* (Fitch).—Fitch, encountering this aphid while selecting roasting ears (*Zea mays*), described it as *Aphis maidis* in 1856. Webster transferred it to *Rhopalosiphum* in 1887. This aphid differs from the apple grain and English grain aphids in its peculiar bluish green color, a deeper blue at the base of the cornicles. It characteristically prefers to feed in the whorls of its hosts. It is common in much of the world between 40°N and 40°S latitude. It extends a little farther north in the United States and into Canada. It first became well known to pathologists as an important vector of sugar cane mosaic virus (33, 229), and it has been reported as a vector of the BYDV by several workers (49, 119, 161, 167, 197, 221, 238, 257).

The corn leaf aphid differs from the other major vectors of yellow dwarf virus in being adapted to slightly higher temperatures. As a consequence, it is found more on warm season grasses. Barley is its only preferred host among cool season cereals. The corn leaf aphid is rare on oats and wheat (266). Its adaptation to warmer weather probably prevents it from being an important vector of yellow dwarf virus in spring-seeded barley (except in unusually late seedings), but this same factor may make it important in early-seeded fall barley.

The corn leaf aphid prefers to feed deep in the whorl of grasses (its only known hosts) and behind leaf sheaths. This somewhat sheltered microhabitat may give it some protection from heavy summer showers, desiccation, and some biological enemies. Honeydew and cast skins of aphids are revealed on the leaf blades as the leaves are exserted from the whorl. When the tassels of corn or the inflorescences of sorghum, both preferred hosts, begin to emerge from the whorl, the aphids congregate on them in abundance. They have produced such copious honeydew on corn tassels that pollen was not liberated. Corn and sorghum breeders have selected varieties unsuited to the rapid multiplication of this aphid (124, 171, 249).

The corn leaf aphid, unlike the other major vectors of the BYDV, has no known egg stage. In 20 years of observations, Wildermuth and Walter (266) found no oviparous females, nor have other students of this species in other parts of the world. Males have developed in the laboratory (266) and in old caged cultures in the greenhouse (55). Eastop found them in nature in Kenya (78). A 15°F freeze at Tempe, Ariz., killed at least 75% of these aphids. Wildermuth and Walter believe this is about the lowest temperature the species can ordinarily tolerate. Corn leaf aphids,

however, survived a 1°F freeze at Lind, Wash., in November, 1959, after exposure to weather that was favorable for hardening; but they died off during subsequent days of alternate freezing and thawing. In regions in which it winterkills, this aphid depends upon migration from more southerly points.

Normally, 2 major migrations of the corn leaf aphid a year take place in Arizona and Texas (266). The first migration begins about March 25, the second about August 25. Each lasts about 6 weeks. These dates probably mark the decline of the cool and warm season hosts, respectively. Bryson (48) in Kansas noted that the corn leaf aphid appears on sorghum about May 10, which is as early as this host emerges from the soil. It is primarily a sorghum aphid, going to corn just before the latter host tassels. Two major summer flights occur (about July 1 and August 1) in Kansas. As corn or sorghum matures or is damaged by frost, the aphid usually migrates to fall barley seedings. As the barley matures or declines seriously in the spring, the aphid migrates to sorghum and corn. If this sequence describes the origin of most of the corn leaf aphids that fly to barley, chances are that many of them arrive nonviruliferous, since corn (?) and most sorghums (?) are not important hosts of the yellow dwarf virus.

Its characteristic bluish-green color, the habit of feeding deep in the whorls, and production of abundant honeydew should help pathologists make tentative identifications of this species.

THE ROSE GRASS APHID.—*Macrosiphum dirhodum* (Walker).—This vector of the BYDV (161, 167, 184, 257) has received comparatively little study. It is a rather large, light yellowish-green, pale aphid with pale antennae that seems to prefer oats and often feeds with its body oriented parallel to the venation of the host. This aphid scatters over the foliage like the English grain aphid, not concentrating near the soil line like the apple grain aphid may do and not feeding in whorls like the corn leaf aphid. It falls from the host plant with only slight agitation. It appeared about the same time of year as the English grain aphid in California (168). Observations in western Washington (43) show that the rose grass aphid may be fairly abundant in fall and early spring, suggesting that it is tolerant to cool temperatures. Dickason, *et al.* (75) found this species the most abundant aphid on spring barley in western Oregon in 1959.

According to Oswald and Houston (168), the rose grass aphid is relatively inefficient as a vector of the BYDV in California, but in Germany it was highly efficient (184). Orlob (159) found that it was less efficient than the apple grain aphid in Wisconsin. The rose grass aphid is a known vector of the BYDV in Washington (unpublished), and it is effective in England (256, 257). Broadbent and Doncaster (36), in England, noted this aphid left the rose for its grass hosts in June and July, much too late to make aphids arising from eggs of importance in epidemiology of BYD in England. Orlob and Medler (163) did not find overwintering forms on *Rosa* sp., but did find eggs on heavily infested barley in the greenhouse. This aphid species, like the others, is probably of significance in spring cereals only where it overwinters as ovoviviparae or blows in at an early date. It was abundant in summer on *Phalaris* sp. in Wisconsin (163).

THE BLUEGRASS APHID.—*Rhopalosiphum poae* (Gillette).—The bluegrass aphid seldom moves to grain and therefore is of no importance as a vector of the BYDV from bluegrass to cereals.

Orlob (160) did not find this aphid in Wisconsin until fall, when it occurred on bluegrass (*Poa pratensis*) near the ground, where it apparently plays a role only in moving virus about in the bluegrass. Orlob and Medler (163) did not find it on *Lonicera* sp. The bluegrass aphid differs from the others in having long, gracefully arching, conspicuous antennae; and in being dusky brown or shining black, with pale cornicles. It infests lawn and wild grasses in Colorado and New Mexico (94).

Post, *et al.* (182) and Orlob and Medler (163) have prepared a simplified key for the identification of aphids of interest to students of BYD.

It is interesting to note that several of the great biologists of the world have contributed to our knowledge of the BYDV-aphid complex, at least in an indirect manner. Carolus Linnaeus described a great many common and important insects, among them *Rhopalosiphum padi* (L.), the bird-cherry oat aphid. The English grain aphid may have been described by a Danish student of his, Johann Cristian Fabricius, as *Aphis avenae* Fab. William Kirby, educated for the clergy and rector of Burham, called the father of English entomology, is known to have described the widespread English grain aphid [*Macrosiphum granarium* (Kirby)]. Another great English entomologist and one who described many insects of the New World, Francis Walker, named *Macrosiphum dirhodum* (Walker), the rose grass aphid. And the first American entomologist to be employed by a state (New York) described *Rhopalosiphum maidis* (Fitch), the plum grain aphid. Brief biographical sketches of these and other famous entomologists are given by Essig (91).

VECTOR-FEEDING RELATIONSHIPS

In discovering the BYDV, Oswald and Houston (167) proved that those grass-feeding aphids that were available to them for study were vectors. They further demonstrated that upon becoming viruliferous, aphids remained so for life, and that a single viruliferous aphid could infect a plant. They also discovered that nymphs are virus-free at birth. and this has been verified by all workers who used Oswald and Houston's (167) methods. Toko and Bruehl (245) found nymphs as effective vectors as adults. Orloh (159) and Watson and Mulligan (257) found that the virus persists through molting (ecdysis).

Although all investigators to date (6, 159, 167, 195, 238, 244, 259) agree that the virus persists in the vector, the details of acquisition, inoculation feeding periods, and possible latent periods in the vector are less well estabished. According to Allen (6), Freitag obtained acquisition of virus in 5 minutes, using the apple grain aphid. He ohtained infection of healthy seedlings when viruliferous aphids were allowed an inoculation feeding of 5 minutes. Rochow (195), using single aphids, found that acquisition periods of 1 hour resulted only in occasional transmission, but demonstrated persistence of the virus in apple grain and English grain aphids for life, following 24-hour acquisition feedings. Watson, *et al.* (259) reported that the bird-cherry oat aphid must feed more than a day to acquire and more than a day to inoculate, if transmission is to occur in a high proportion of insect movements. Watson and Mulligan (257), in a later trial using the bird-cherry oat aphid, reported occasional acquisition in 30 minutes and a rare inoculation in a test feeding of 15 minutes. The minimum time required for the entire process of transmission was 10 hours. and 32 hours were needed for ahout half the aphids, able to acquire virus and transmit it, to do so. Toko and Bruehl (245), working with only 2 strains of the virus and with single aphid collections, failed to obtain transmission when the apple grain or English grain aphids were allowed acquisition periods of 16 hours or less. Acquisition feedings of 24 hours were adequate. Likewise, they failed to obtain transmissions if inoculation feedings were short (less than 1 hour 40 minutes).

Orlob (159) failed to obtain transmission using the apple grain aphid in acquisition feedings of 10 minutes. He obtained infection of 1 plant using a total of about 515 aphids that had been allowed acquisition feedings of 1-2 hours. When this species of aphid was allowed at least a week on a source plant, inoculation feedings became successful in 30 minutes (3 plants of 7, using 5-10 aphids/plant). The rose grass aphid required 1-hour inoculation feeding periods before transmissions began.

For best transmission, the acquisition period should be at least 24 hours and the inoculation feeding at least 4-8 hours, or hetter, 24 hours in routine work. Although an occasional aphid accomplishes an acquisition or inoculation quickly, this unusual feat prohably has little effect on epidemiology, except under conditions of great numhers of migrants.

The BYDV is systemically distributed in the host. This is evident from the fact that the parts of the plant on which the aphids feed do not seem related to acquisition of virus. For example, the apple grain aphid at times tends to feed near the soil line; the English grain aphid scatters over the aerial portions of the plant in plain sight, often congregating in the inflorescences; the rose grass aphid favors leaves well above the soil line and tends to align itself parallel to the midrib; the corn aphid thrives deep in the whorls and behind the leaf sheaths of barley. Yet, all of these transmit the virus readily. Toko and Bruehl (245) caged aphids on specific leaves, including the youngest that did not yet express symptoms. Transmission was not influenced by the position of feeding. Orlob (159) recovered virus from roots of infected plants using the apple grain aphid, but his attempt to inoculate by feeding viruliferous aphids on roots apparently failed, providing additional evidence of virus-movement via phloem.

Orlob (159) was ahle to introduce virus into the rose grass aphid by the mechanical transfer of the haemolymph from a viruliferous aphid of the same species (3 transmissions in 370 attempts), and Mueller, *et al.* (155) were highly successful in their inoculation of apple grain and English grain aphids, rendering a large proportion of them viruliferous. This mechanical transmission of virus from aphid to aphid has been accomplished for other aphid-virus associations (74, 117, 120).

To date, all forms of these aphids that normally feed on grasses have been capable of transmitting the BYDV. When Orlob and Arny (162) studied the various forms of the apple grain aphid that normally feed on the apple, however, they discovered that all developmental stages of a vector are not necessarily potential vectors. The sexuparae, males and alate fundatrigenae. failed to transmit the virus when fed on diseased barley and then transferred to healthy barley. One stage, the fundatrices, even refused to feed on the grass host. Oviparae and nymphal fundatrigenae manipulated in the above manner were vectors. Prohably, the failure of most of these attempts was due to the deep-seated adaptation of these stages to the apple; or possibly, in the case of the sexuparae or males, to reduced feeding and assimilatory activities. Kennedy and Stroyan (133) pointed out that some of the highly differential sexual forms of aphids do not feed at all.

Exploratory researches to date prove the existence of great variation within the BYDV. Various isolates of the virus studied in detail differ in their relative virulence on different varieties of oats, wheat, and barley (6). They differ also in their ability to infect different grass species and genera, and in the symptoms they produce (47, 195), as well as in their transmission by different aphid vectors (197, 221, 245). There is no cross-protection between strains, either in the vector (6, 256) or the host plant (6, 195, 245, 256). Although Rochow (193) has recently obtained transmission by feeding aphids through membranes, *in vitro* studies have not as yet been performed; and the physical properties of the virus are not known. For the present, this collection of variants is considered a working unit and the BYDV strains will be reviewed here according to the methods of differentiation.

Strains as Determined by Differential Virulence on Cereal Varieties.—Strains identified either on the basis of grass hosts (other than oats, wheat, and barley) or on the basis of vector relations are of significance, since they may influence epidemiology. Strains detected by differential virulence on varieties of the small grains are especially important; they will surely plague workers dedicated to the control of yellow dwarf through breeding. Bruehl and Toko (46), Takeshita (236), and Raymer (unpublished) observed differences of this type, but the only comprehensive work on the identification of strains of differential virulence to the major cereal hosts is that of Allen (6).

Allen first studied 31 varieties of cereals (13 barleys, 11 oats, 6 wheats, 1 rye), using a few isolates of the virus to locate suitable differential varieties. He finally selected 3 barley varieties (Black Hulless, Rojo, Atlas 46), and 1 oat variety (Coast Black). Forty-three isolates of the virus from California and several other states then were studied on the differential varieties. Using stunting and discoloration as the criteria, the 43 isolates were divided into 16 strains. The 16 strains could be classified as belonging to 7 "types" (Table 3) on the basis of their ability to discolor each of the 4 differential varieties.

Testing for resistance in screening and breeding projects has not yet advanced to the stage of using several diverse strains of the virus on a systematic basis. Endo (85) used a moderately virulent strain in his studies of resistance in oats. Most workers, however, are using natural field epidemics as a basis for determining varietal resistance, without regard to strains.

Table 3. Classification of 7 "types" of the BYDV as determined by pigmentation of the host (Allen, 6)

Differential variety	BYDV type I	II	III	IV	V	VI	VII
Black Hulless	C[a]	C	C	C	O	O	O
Rojo	C	O	O	C	O	O	O
Atlas 46	C	C	O	O	C	C	O
Coast Black	C	C	C	C	C	O	C

[a] C = variety discolored, O = no pigment reaction to infection.

Table 4. A tabulation of genera and species, showing the differential host range of 6 strains of the BYDV

Test species	Virus strains: Calif.[a]	Wash. original	Wash. EG	Ill.	NY AG	NY EG
Phleum pratense L.	—[b]	+	++	+	+	—
Lolium perenne L.	—	—	++	+	+	+
Bromus inermis Leyss.[c]	++	—	—	+	—	—
B. inermis (var. Manchar)		—	—	—	—	—
Bromus catharticus Vahl	++	++	++	—	—	—
Dactylis glomerata L.	+	+	+	—	—	—
D. glomerata (var. Dwarf)		+	++	++	+	—

[a] California, results of Oswald and Houston (168); Washington, Bruehl and Toko (47); Illinois and New York, Rochow (195).

[b] — indicates immune; +, symptomless carrier; ++, symptoms with recovery of virus.

[c] The smooth brome accession of California, undetermined; that of Bruehl and Toko and Rochow, P-3053.

Strains on the Basis of Host Range.—As briefly mentioned in the section on host range, and as illustrated by the differing host reactions presented in Table 2, strains of the BYDV may be differentiated on the basis of their individual host ranges. When host ranges determined by independent studies in Washington (47) and California (168) were compared, not only were they different, but the 2 strains of the Washington virus also differed from each other in their host ranges.

Marked genetic variation exists within many grass species. Although the 2 Washington strains of the virus were tested simultaneously on the same grass accessions, gross comparisons of results such as those obtained in Washington and California, where different accessions of grasses were used, could lead to misinterpretations. In some cases, the differences were probably due to differences in the host, rather than in the virus. Rochow (195) partially resolved this by obtaining seed used in the Washington study and subjecting plants derived from it to different strains of the virus. This more critical comparison of host ranges, using different strains of the yellow dwarf virus, confirmed the interpretation that strains of the virus might differ in host ranges on the genus and species level (Table 4).

Smooth brome (*Bromus inermis*) was reported as severely damaged in California (168) and a host in Ontario (222). In Washington (47), it was immune to 2 strains. Rochow (195) found it immune to 2 New York isolates and a symptomless carrier of an Illinois strain. Timothy (*Phleum pratense*) was immune in California; in Washington, 1 strain produced symptoms on a variety of this host and another variety was a symptomless carrier or immune, depending on the virus strain. Slykhuis (220) and Slykbuis, *et al.* (222) found naturally diseased timothy with typical symptoms of yellow dwarf. Additional evi-

dence of differences in host range of strains of the virus can be found in the section on host range. Differences in host range could easily affect the adaptability of a given virus strain to a region; not only because certain grasses prevalent in that region might not be susceptible to a particular strain, but also because a host susceptible to that strain might be avoided by aphids prevalent in the region.

The data in Tables 2 and 4 clearly show that individual strains of the virus might differ in their host ranges. Rochow (195) treated his species on an individual plant basis. In some grasses, he encountered individual plants differing from others within the same species. Oswald and Houston (168) had already encountered such differences in the agronomically purified *Sorghum vulgare* varieties tested (1 was a symptomless carrier; a closely related variety was immune). Also, Allen (6) found that some virus strains failed to discolor certain cereal varieties.

The differing host ranges of different strains of the virus, however, should not be over-emphasized. It must be kept in mind that the many strains differing in host range and vector relationships already discovered have a common core of similar host reactions upon which their inclusion as strains of the yellow dwarf virus rests.

The millet red-leaf virus, a yellows-type, aphid-borne virus of grasses in China (269), suggests that if sufficient studies were made around the world, a more or less continuous series of strains of aphid-borne virus would be discovered having gradually overlapping host ranges. *Setaria lutescens* was a host to the English grain strain of the BYDV in the Washington study (47) and it is a host in Wisconsin (159). *Setaria viridis* became reddened and purpled when viruliferous aphids were fed upon it, but in no case was virus recovered from it (47). Marion Watson (254, 256) reported infecting corn with the BYDV in England. These fragmentary observations do suggest, however, that a "slight" change in the virus could accomplish the shift to new hosts. Until more is known, however, cereal pathologists will do well to retain oats, barley, and wheat as the major hosts of strains considered the yellow dwarf virus.

Strains as Determined by Vector Relationships.—Oswald and Houston (167) demonstrated that several aphid vectors of the yellow dwarf virus differed in efficiency on the basis of numbers of plants infected. In a preliminary trial in Washington (46) with a single virus collection, the apple grain aphid was a more efficient vector than the English grain aphid. There were greater differences, however. The

Fig. 5. Strains of the BYDV vary markedly in virulence on Club Mariout barley (left), Idaed wheat (center), and on Bannock oats (right). These 3 spring cereals were inoculated with the apple grain strain (245) (left-hand bundle of each trio) and with the English grain strain (center bundle of each trio). The right-hand bundle is the healthy control. Note the extreme sterility in the oats inoculated with the severe strain. Each bundle contains the same number of plants. Cereals grown outdoors at Pullman, Wash., 1957. Photo, courtesy of H. V. Toko.

plants infected by means of the apple grain aphid were more severely stunted and developed stronger coloration than those infected by means of the English grain aphid. This difference in efficiency of transmission and virulence of transmitted virus persisted in serial transmissions. Increasing the number of aphids/plant from 1 to 8 did not increase the severity of the disease, with either the English grain or apple grain aphid. It was concluded that the difference was not quantitative, but that the apple grain aphid in this case transmitted more virulent virus than the other aphid.

This qualitative difference in virus transmitted by the 2 aphid species led to the speculation that vector specific strains might exist. In succeeding tests of 34 virus isolates, 1 was found that was transmitted only by the apple grain aphid and another was transmitted only by the English grain aphid (245) (Fig. 5). The vector specificity was a stable quality in serial transfers. Inoculating the same plant with both viruses gave no evidence of interference; both isolates were recovered still vector-specific.

While the bulk of the isolates in Washington (32 of 34) (and apparently, Illinois, California, and several other states) were not vector-specific, Rochow (191), in New York, found that most of his isolates were transmitted by the English grain aphid and rarely or not at all by the apple grain aphid; a few by the apple grain aphid and rarely or not at all by the English grain aphid; and only a few, with facility, by both. This suggested a possible regional difference in virus-vector relationship, due to differences in the virus complex or to the insects themselves. To resolve this problem, nonviruliferous aphids of both species were exchanged and used in parallel studies in both New York and Washington The indications of vector specificity of a high degree in the New York virus isolate were verified by this study. The virus in New York (192) remained, for the most part, vector-specific; in Washington (42), a new series of isolates was entirely nonspecific, transmitted by either species, whether New York or Washington aphids were used. Slykhuis, *et al.* (221) found vector-specific isolates in Ontario, using the bird-cherry oat aphid and the English grain aphid. Orlob's (159) Wisconsin strain was transmitted by both apple grain and English grain aphids. Watson and Mulligan (256, 257) found some isolates incapable of transmission by the bird-cherry oat aphid, but little other evidence of vector specificity.

Rochow's (195) contributions indicate that the vector specificity of most of his virus isolates is relative rather than absolute. When virus was transmitted by the "nonvector" aphid, it could have been due to a mutation or selection of 1 component from a mixture. If this were the case, the virus thus transmitted should be transmitted with high frequency in subsequent feedings of the "nonvector" species. Rochow tested this hypothesis and found that the virus-vector relationship of the parent isolate was unaltered by its rare transmissions through the "nonvector" species. Watson and Mulligan (257) confirmed this relationship. Vector-specificity was a stable character of the virus strains in question.

When the apple grain and English grain strains of virus, used by Toko and Bruehl (245), were introduced into the same host and subsequently transmitted to other plants, they were unaltered by coexistence in the same plant: they were still vector-specific when removed. In a similar trial, Rochow (194), using New York virus, obtained a different result. When plants were doubly infected with relatively vector-specific strains, the English grain strain was recovered as introduced; the apple grain aphid, however, recovered virus subsequently transmissible by it and the English grain aphid. This difference in behavior of mixed strains has not been explained.

Recent studies by Rochow (197, 278) show that vector-specific strains are widely distributed in nature. So far, he has discovered corn leaf, apple grain, and English grain aphid-specific strains scattered through Florida, Georgia, North Carolina, Mississippi, Texas, California, Missouri, Illinois, Iowa, Minnesota, Wisconsin, Pennsylvania, and New York.

The ability of a virus strain to be transmitted by several rather than 1 or a few vector species should favor survival of the virus, particularly where species may vary in populations from year to year or season to season, or even more often (245). In addition to influencing epidemiology, vector-specificity could easily lead plant pathologists astray. For greatest safety in diagnosis, more than 1 aphid species should be given an opportunity to recover virus from a suspected host. In the same light, an aphid species might be classed as a "nonvector" on the basis of tests with 1 virus strain, when in reality it is a vector for another strain.

Introduction of more than 1 strain into a plant apparently does not influence disease development beyond that of the more virulent strain alone. This is interpreted as evidence of close relationship among such strains (6, 24, 122, 194).

A section on epidemiology should bring together the many factors affecting disease development. It should synthesize them into a coherent narration. The complexity of this disease, with so many important gaps in our present knowledge, will prevent detailed treatment of epidemiology for some time to come. The role played by each aphid species is dependent on the time of initial buildup, its abundance and movements, and its ability to transmit virus strains. The role of the various reservoir hosts, the strains of virus they sustain, their relative palatability to a given species of aphid, and the timing of these periods of palatability with the stages of development of the cereal hosts need to be known. An effort will be made to present some of the factors that operate in epidemiology, and to give a description of the Pacific coastal areas of the United States in relation to BYD.

Need for Rapidity of Spread.—Van der Plank (246), in discussing "Some epidemiological consequences of systemic infection," concluded that systemic diseases "multiply" or affect additional individuals rather slowly in any given planting. His examples included studies of virus-spread in orchards where 1 tree is infected in year 1, another in year 2, several in year 3; until after a period of years, quite a few trees are involved. In some respects, his choice of examples is poor, because there are several systemic diseases in field crops that can spread rapidly and involve many individual plants in a short time. Among them could be listed mosaic and ratoon stunt disease of sugar cane; rice stunt; wheat streak mosaic; common bunt [*Tilletia caries* (D.C.) Tul.], in which smut spore showers are effective in the life cycle in the Pacific Northwest of the United States; curly top of sugar beets; and some of the virus diseases of English peas (*Pisum sativum* L.). BYD is also a systemic disease of real epidemic capability.

It appears more logical to attribute the slow spread of some systemic diseases to specific weaknesses in the disease cycle, rather than to the characteristic of being systemic. An acre of wheat, oats, or barley contains about 650,000 plants. These hosts, particularly when seeded in the spring, complete their vegetative development in a few months. If yellow dwarf is to become severe, most of these 650,000 plants/A must be infected within 3-4 weeks after emergence from the soil. An extensive migration of viruliferous aphids is required to disseminate the virus rapidly through the many seedlings of extended acreages, even entire sections of states. Recorded epidemics of yellow dwarf are mute evidence of such massive transmission. Unquestionably, in their quiet way, aphid vectors of the BYDV perform a tremendous feat of transmission.

Major Aphid Migration in Relation to Epidemiology.—The land mass of North America offers many advantages in a study of epidemiology. The grass cereals are cultivated from within Mexico, across the interior of America, and into southern Canada. Between the cultivated grasses, areas of range and pasture grasses help to form an extended band of more or less acceptable host material for migrating aphids. The climate varies considerably from south to north and to a lesser degree from west to east. As it is a continental land mass, this region is exposed to marked seasonal and daily fluctuations in temperature, wind, and humidity (Fig. 6). Cooperation among observers of the region also contributes to the value of this outdoor laboratory.

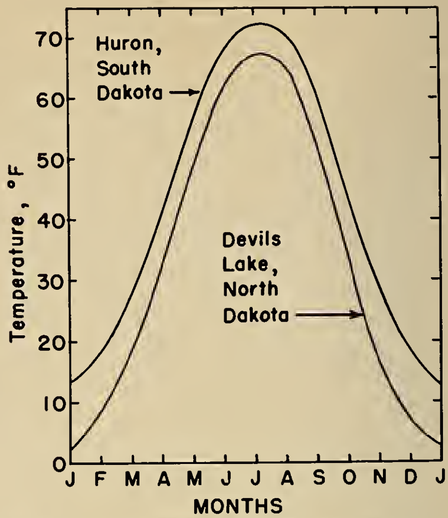

Fig. 6. The seasonal rise and fall of mean monthly temperatures is abrupt in the north central United States. The physical environment is so severe that only a brief season is favorable for grain aphid multiplication. Succulent small grain becomes available about the time the mean monthly temperature line reaches 45-50°F. It then passes rapidly to 65°F, at which point biological enemies are supposed to dominate. The period of coexisting favorable temperatures and succulent forage is so short that sizeable grass aphid populations in a "typical" season in this region are dependent on migrations. Conditions here are in marked contrast to those of the Pacific Northwest depicted in Fig. 9, 10, 11. It is believed that these differences in the physical environment play a major role in determining the frequency with which BYD develops in the Pacific Northwest and its relative infrequency in the north central plains region.

The greenbug (Fig. 7) and the corn leaf aphids are migratory species that overwinter in regions of moderate winters such as in northern Texas and Oklahoma; and, if favorable conditions prevail, migrate far to the north, even into southern Manitoba and Saskatchewan. This northward movement depends upon proper synchronization of environmental conditions and aphid stages (Fig. 8), making possible a succession of individual flights of 50, 100, or even 200 miles each (163, 248, 274). Aphids apparently have been blown from the mainland of Eurasia to Spitsbergen, 800 miles away (80).

The ability of the greenbug to destroy wheat and oats (according to Walton (251), 70% of the wheat of Texas was abandoned in 1907) has led entomolo-

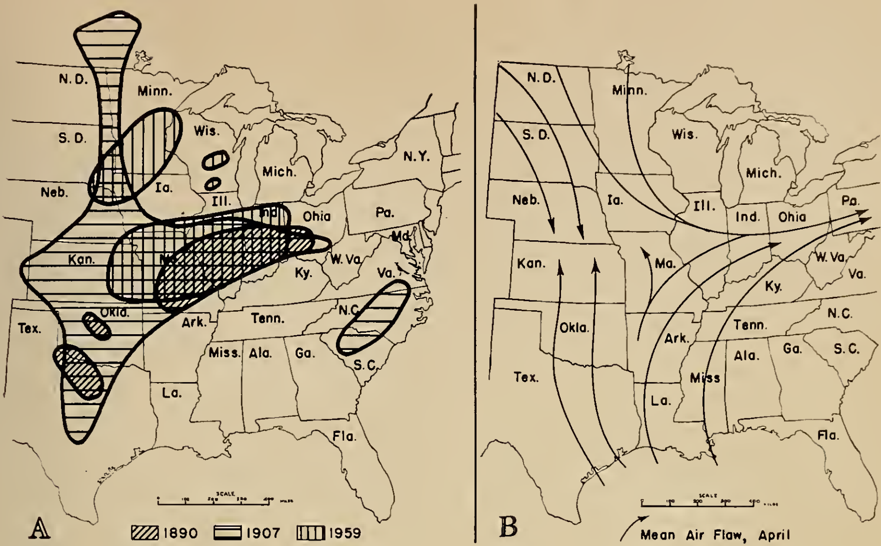

Fig. 7. Left, the migrations of the greenbug from northern Texas and Oklahoma northward up the plains and eastward below the Great Lakes reflect air movements at the time wings develop on great numbers of individual aphids. The migrations of 1890, 1907 (263), and 1959 (156, 274) took 2 major paths: northbward and northeastward below the southern tip of Lake Michigan across Illinois and Indiana. The eastward thrust of the migrations below the Great Lakes probably results from the strong deflection of the winds (right) entering North Central United States by these inland bodies of water (data taken from Orlob, 159).

gists to subject this aphid to close observations. Outbreaks are most common in northern Texas and Oklahoma where they usually follow summers with rains favorable to the establishment of volunteer grain, a mild winter permitting ovoviviparae to survive in large numbers, and a cool backward spring with few hard-driving rains. The greenbugs tend to feed and multiply in 1 place, where they reach the limit of the host. Just prior to death of the host, many greenbugs become winged. A south wind at this time initiates the northward migration.

The aphid movements from this area are not guided northward by "intelligence." If the winds blow to the south, the insects find themselves on more advanced grain that not only does not support such multiplication but also is not so easily damaged. If it drifts them far to the west, the insects may find themselves, for the most part, deposited in regions of considerable aridity and little succulent forage. If wind blows tbem far eastward, they are usually decimated by the frequent hard-driving rains that fall during cool months in this area. To the north, they encounter seedling wheat and oats (Fig. 8), their preferred host plants. On alighting, the greenbug is believed to remain in its new habitat and reproduce there. The original winged parents do not go successively northward with intermittent rests. The next major northward migration is made by offspring of the second or subsequent generations.

The corn leaf aphid, lacking an egg stage and unable to survive prolonged periods of cold weather, occurs in the northern interior of North America following similar migrations from the south each year.

An evaluation of these major greenbug and corn leaf aphid migrations in relation to BYD is difficult at present. Several observations support the role of the greenbug as a major vector. In California, the greenbug and corn leaf aphid were adequately efficient vectors (167). The greenbug was a good vector in Mississippi (230). In Illinois, several collections of greenbugs in the epidemic of 1959 (Fig. 7) were viruliferous (127). In Texas (17), Missouri (241), Kansas (217), Illinois (127), Indiana (52), Wisconsin (161), and North Carolina (119), in the same epidemic, observers considered the greenbug a significant factor.

Contrary to the above observations, in extensive transmission trials using diseased oats from several states, Rochow (197) found Florida greenbugs to be vectors of virus from only 2 leaf collections (both from Florida) out of 127 that contained virus transmitted by 1 or more aphid species. Rochow (198, 277) has more recently discovered strains of tbe greenbug that differ in their ability to transmit virus; hence, the low recovery in former tests could have been due to the use of a "wrong" strain of greenbugs. It might also be significant that greenbug-resistant

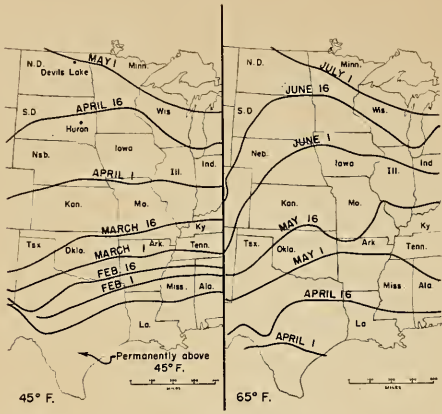

Fig. 8. The advance of warming, south to north, in the central western plains of tbe United States, is shown by the isotherm lines of the average date at which a daily mean temperature of 45°F is reached (135). These lines can be used to visualize the beginning of real aphid activity and the appearance of the spring flush of growth among grasses, followed by emergence of the spring-seeded small grains. Heavy winter survival of ovoviviparae in north Texas and Oklahoma, followed by properly timed south winds, could move the aphid northward in stages timed so as to capitalize on the northward progression of spring. The time favorable for aphids could in this way be extended from late winter on through all of spring, except that the scene of the activity would gradually shift northward. The 65°F isotherm (135) follows about 60 days in the wake of the 45°F level, allowing considerable time for damage before biological controls will dominate. It is fortunate that a cool, moist summer and mild winter in the southwest, essential to establishing the heavy initial population of migrants, is seldom followed by the proper sequence of winds and growing conditions to the north. It should also be noted that a mean daily temperature of 65°F comes early in southern United States. Heat limits grass aphids much of the year in southern areas, either by being directly adverse to the aphids or by favoring their natural enemies. Winter is usually the most favorable season for grass aphids in the south (263).

cereals (16), illustrated in pictures by entomologists, do not appear to be suffering from yellow dwarf.

It is conceivable that yellow dwarf resistant varieties, developed in breeding programs in North Central states, could be susceptible to strains brought in by waves of greenbugs, or other aphid species (?), from states to the south during epidemic years. The ability of the greenbug to act as a vector should be thoroughly studied, especially in Texas and Oklahoma, areas usually implicated as the source of the migrations.

The toxic factor of this species also makes evaluation of yellow dwarf and direct feeding damage difficult. Dahms and Wood (66) estimate that 100 greenbugs/ft of row, the rows 7 in. apart, would be about 7,500,000 aphids/A; and that such a population causes a loss of 1 bu/13-29 days of feeding. This is not a heavy aphid population. Ruggles and Wadley (206) state, for example, that the oats are not killed until the population reaches 2,000-4,000 greenbugs/ft^2.

Migratory vs. Local Aphids.—Close field observations are needed to determine the timing of the appearance of the various species in the field. Washburn (252) and his associates had been alerted to the depredations of the greenbug in the southwestern states in 1907, and of its progress northward. They diligently observed the fields of Minnesota. The greenbug did not appear until 45 days later than the "native" English grain aphid. Wadley (248), also in Minnesota, but during a later period of years, found that species such as the apple grain and English grain aphids became active in late April and May, much earlier than the arrival of the migratory greenbug or corn leaf aphid. In contrast to these records, the greenbug was well into Wisconsin (161, 275) and Minnesota (8, 161, 274) in the first week of May, 1959. This is the earliest migration of greenbug into Minnesota, by almost a month, that has ever been recorded (10). The corn leaf aphid appeared in Wisconsin as early as the apple grain aphid (161) in that year. The first species to bring virus to a host should be the most important, other things being equal. On this basis, species overwintering locally in the area have an advantage in most seasons.

Epidemics originating with migrants probably will be infrequent because extensive migrations depend on a series of delicate environmental conditions. Species that overwinter in an area of potential epidemic are in a position to take advantage of a shorter period of favorable weather. Overwintering in an area also should place them at many points at once so that a "small" spread from each site could result in rapid coverage of a large area.

Migrants can introduce "new" virus to an area, but if local aphids are unable to transmit it and the migrations are infrequent. such a virus could disappear from the region. Even perennial grass plants probably have a longevity limit. Aphids "native" to an area will move the virus frequently from host plant to host plant. This should maintain an adequate reservoir of virus that can be transmitted by these species.

If the individual aphids of a major migration begin their journey already viruliferous, there is little or no danger of exhausting this virus store in their successive flights to fields of healthy seedlings. The virus is fully persistent in its vectors so far as is known (no one has studied the greenbug or corn leaf aphid in this respect) and an individual usually remains viruliferous for life. There is apparently a deep-seated tendency among aphids for winged parents to bear wingless progeny. This is almost absolute in the greenbug (248). The wingless parents may or may not have winged progeny, depending upon conditions. The sequence, 1) winged, 2) wingless, 3) winged or wingless, would insure that the bulk of the aphids in a new field would remain sufficiently long for the plants to become systemically infected and subsequent flights to be made up of viruliferous individuals. No one has determined the minimum time it takes for a plant to become systemically infected to the degree that aphids feeding anywhere on the plant would become viruliferous.

Before leaving considerations of migratory vs. "native" aphids in epidemiology, the years of 1890 and 1907 should be considered. Records show that these years were disastrous for the oat plant in most of the eastern half of the United States. The only plausible explanation for the disaster is that epidemics of yellow dwarf occurred both years. Murphy (156) stated that the epidemic of BYD of 1959 was comparable to epidemics of rust or Victoria blight on oats. Consequently, oat workers should give yellow dwarf serious consideration. If the records are properly interpreted, the losses of 1959 were moderate, when compared with those of certain years of the past. The years 1890 and 1907 were notably favorable to aphids in small grain. Webster and Phillips (263) show that the most extensive migrations of the greeenbug known in early years occurred in those 2 seasons (Fig. 7). But the many observers cited by Manns (144) in his treatise on the mysterious malady of oats stressed the English grain aphid. The greenbug did not cover nearly all, or even a major portion of the area of serious loss. It is more logical to believe that 1890 and 1907 were years of mild winters and prolonged cool springs favorable to early development of grain aphids in general and delaying seedings on a large scale; and that dispersions of the locally overwintered aphids, such as the English grain aphid, accounted for the bulk of the transmission. The apple grain and English grain aphids, used as examples of "local" species, can be blown by wind the same as the migratory species, but the general contrast in life patterns is believed justified.

Overwintering Ovoviviparae vs. Aphids Emerging from Eggs in Epidemiology.—Most students of the grass aphids considered in this paper express the belief that eggs are of little value in initiating an epidemic of aphids (179, 248, 263). It is particularly doubtful that fundatrices could give rise to a large population early enough in the spring to be much of a factor in spreading the yellow dwarf virus. As mentioned previously, the greenbug and English grain oviparae lay few eggs each and the hatch may be very low. Major aphid years usually have followed winters permitting ovoviviparae to overwinter in abundance, or the aphids have migrated in abundance early in the season from a more favorable place.

The greenbug usually does not rely on eggs for perpetuation at points below 36°N latitude (248). Farther to the north (in Minnesota), the egg stage is believed to be practically worthless; the sexes apparently are induced by photoperiod changes taking place in late summer (248), and the development of the sexes and oviposition require more time than exists before the onset of steady low temperatures halts all development.

The apple grain and bird-cherry oat aphid overwintering as eggs on the primary host also appear to develop too slowly to cause serious and widespread development of yellow dwarf. Slykhuis, *et al.* (222) in Ontario, found that the bird-cherry oat aphid was nonviruliferous when it left the primary host. Hatching in 1959 began about April 17, but *R. padi* was not observed in the oats until June 12. In 1958, *R. padi* was easily found on oats, barley, and wheat (221) from late May on; in that season, yellow dwarf was more prevalent near primary hosts. But the levels of early spring infection (from all vectors) of oats in these studies were low (15% infection in the Ottawa Valley by mid-July in 1958, and between 1 and 5% of the plants of most oat fields expressed symptoms by mid-July in 1959). Orlob (159, 163), in Wisconsin; and Rademacher and Schwarz (184), in Germany, found aphids in the grain before they had left the primary hosts, indicating that the early invaders of the grain originated from parthenogenetic individuals. The limited observations to date support the theory that ovoviviparae, where they survive the winter or are blown in, are a far greater threat because of their earlier development, wider distribution, and greater numbers; and because they never leave a grass host and are likely to be viruliferous at the outset.

Further evidence of the importance of conditions favoring overwintering is provided by Marion Watson of England (254). When first observed there, this disease was considered of academic interest only. But a mild winter, 1956, was followed in 1957 by the earliest and largest spring migration of aphids ever recorded, and economic losses followed. The aphids were still abundant in the fall of 1957, and winter oats seeded at that time were seriously affected. In this case, the bird-cherry oat aphid was the most efficient vector.

Reservoir Hosts.—To be of greatest value, a reservoir host should grow enough to shelter aphids during the winter and to provide good forage for them early in the spring so that aphids are nourished before spring seedlings are available. To provide for heavy infection of fall-seeded cereals, the aphid should have a succulent host during the hot, dry summer. None of these aphids is known to lay eggs to escape the danger of desiccation, so a dearth of succulent forage constitutes a major hazard where summer drought is severe. Results of host range studies (for both virus and aphids) can be misleading in that they indicate a great number of hosts, whereas in nature a relatively few can play an important role in the disease cycle.

The importance of a grass as a reservoir host depends on the strains of virus that it harbors; its longevity when infected; its palatability to aphids, particularly at times of the year when the oats, wheat, and barley are not young and succulent; and the density of the sward during the winter. Webster and Phillips (263) and others have noted that fields of winter cereals are often bleak in contrast to the protective sods of bluegrass (*Poa pratense* L.). Slykhuis, *et al.* (222) list timothy, smooth brome, Kentucky bluegrass, red fescue, perennial ryegrass, and intermediate ryegrass as possible sources of the BYDV in Ontario. *Festuca arundinacea* was a major source of rose grass and apple grain aphids in western Oregon in 1959 (75). The aphids departed from the headed grass in swarms to invade seedling spring grass, whereas their departure from winter cereals was more gradual, and extended over a period of time.

According to my observations in western Washington, however, green cereals have consistently maintained greater aphid populations than grasses in the vicinity of the grain fields. Orlob and Medler (163) found the cereals to be the major hosts of the main vector of the BYDV in Wisconsin. When the winter cereals, seeded in late summer or early fall, make rank growth before onset of cold weather, they can constitute a formidable source of aphids and virus.

Infection Pattern Within Fields.—The distribution of and apparent time of infection of diseased plants should give some clue as to the source of the trouble. Diseased plants may be scattered sparsely at random in a field, indicating a small, well-dispersed flight (222) that did not develop further. They may be clustered in spots, indicating primary infections with limited dispersal of apterae. Infected plants may be more abundant along grassy fence-rows (134) or near primary hosts (221), which is evidence of local origin with limited development. Entire fields may be completely (prevalence 100%) diseased and simultaneously infected for all practical purposes (43), indicating massive invasion of viruliferous alatae (winged aphids).

EPIDEMIOLOGY ON THE PACIFIC COAST

California Epidemic, 1951.—The sequence of events leading to the epidemic of yellow dwarf in California in 1951 (168) is well-chronicled, and clearly illustrates the requisites for an epidemic of this disease. The assumption is that the virus was not newly introduced to California, but was widely distributed among the grasses of the state prior to the epidemic. The winter and spring of 1950-51 were cloudy and damp, the weedy winter annual grasses made rank growth, and the aphids multiplied vigorously on this lush food source. The dampness and rainy weather persisted without a dry period until March 7, 1951, after which no rain fell until April 25, the longest spring drought on record in the Sacramento Valley. Farmers, who had been prevented from seeding barley in December, the normal time, hurriedly seeded the fields as they became dry enough to permit tillage. Seeding was virtually complete by March 20. The lush grass of the prolonged moist period rapidly became unpalatable under the drought conditions and the aphids departed in large flights in late March and early April. They found and relished the succulent seedling grain. By late April, yellowing was reported widely distributed in the Sacramento and northern San Joaquin valleys. It was this early infection that triggered the epidemic and its resultant large losses.

By contrast, even though actual precipitation in the next season, 1951-52, was greater, open weather permitted seeding of the barley in December. Aphid dispersals of magnitude did not occur until April, but by that time the grain was heading. Infection occurred, but at this late stage of development there was slight loss.

Oswald and Houston (168) observed the apple grain aphid to be the most common aphid in the winter months; the English grain and grass aphid to appear a little later; and the corn leaf aphid, last.

Endemic Yellow Dwarf Area of Western Oregon and Washington.—The region of Oregon and Washington west of the Cascade Mountains has humid, cloudy winters of moderate temperatures (Fig. 9-11).

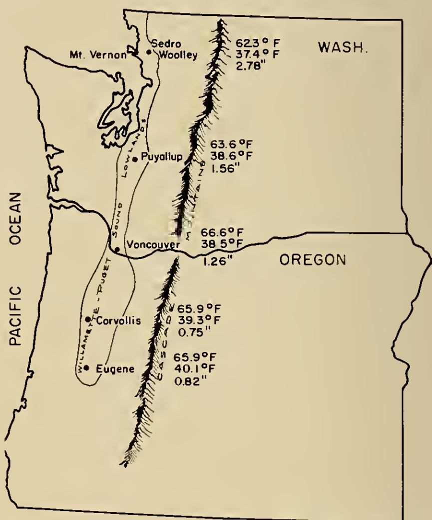

Fig. 9. The "endemic" yellow dwarf area of the Willamette Valley of Oregon and the Puget Sound Lowlands of Washington lies just west of the Cascade Mountains. This is the only agricultural area of any size with moderately cool summers and mild winters in the United States. The mean temperatures in July, the hottest month, vary from 62.3°F at Sedro Woolley to 66.6°F at Vancouver (the top figure of each trio). The mean January temperature ranges from 37.4°F in the north to 40.1°F at the south (the central figure of each trio). Thus, the temperatures are tolerable to the grain aphids most of the year. The aphids are sharply curtailed in the summer, however, by a dearth of succulent foliage. The total July and August precipitation averages 2.78 in. in the north and 0.82 in. in the south (the lowest figure of the trio). In spite of the latter factor, however, this region probably possesses the best physical environment for maintaining aphid populations in the United States; and this is a large factor in explaining the frequency with which BYD occurs in the small grains of this region.

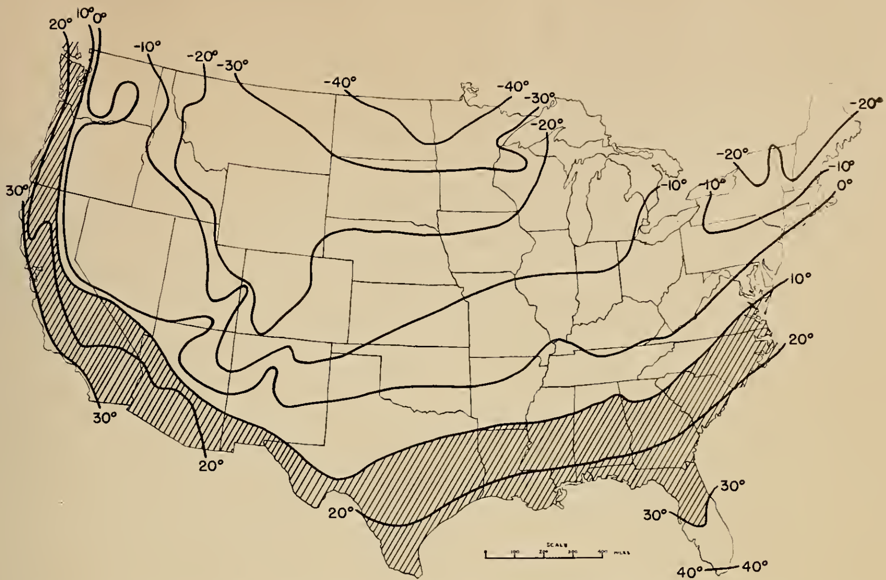

Fig. 10. Isotherms of average minimal annual temperatures in continental United States. Observations indicate that ovoviviparae of the grass aphids survive the winter in limited numbers in regions in which the minimum temperatures are about 10°F. If this generalization be widely true, aphids could be normally expected to be present in early spring in the entire Pacific coastal region and eastward across the southern portions of the United States. Overwintering of any number of ovoviviparae in regions of more severe winters could be expected only when the season is more mild than normal.

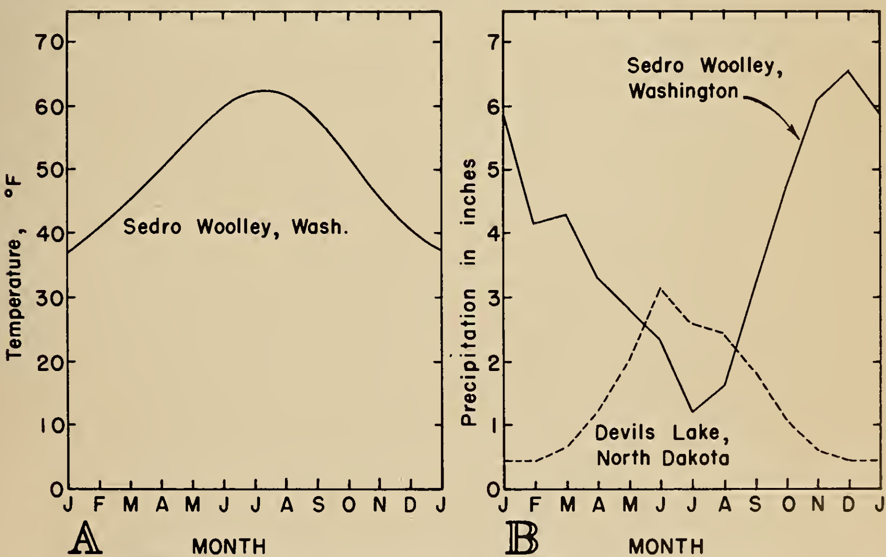

Fig. 11. The rise and fall of mean monthly temperatures at Sedro Woolley, Wash. **A)** are gradual, never extremely cold or hot, but remaining for the most part reasonably favorable to grass aphids. The rainfall at this location (solid line, **B**) is heavy in the cool months, light in the summer. The moderate winters tend to permit ovoviviparae to survive; the cool, long wet spring permits them to multiply; the high soil moisture prohibits tillage, and delays spring seeding, making a combination favorable to infection of grain at an early stage of development. This condition commonly prevails throughout the Puget Sound-Willamette Valley lowlands system. At a similar latitude in north central United States (Devil's Lake, N. D., shown by broken line, **B**), the cool months are dry and tillage and seeding usually proceed rapidly when temperatures permit.

The apple grain, English grain, and rose grass aphids usually overwinter in limited numbers in grasses and early-seeded fall cereals as ovoviviparae. Temperatures rise in early spring, but planting is delayed because of the wetness of the soil (Fig. 11). The aphids multiply during this period of cool weather. By the time the soil can be worked and seeded in the spring (43, 187), apple grain, English grain, and rose grass aphids are ready, in many seasons, to migrate into the young grain. In this region, the aphid population is usually adequate for transmission of the yellow dwarf virus throughout the season. Consequently, planting date, as a means of avoiding the disease, is of minimal value. Yellow dwarf is known to have been serious in 1955, 1957, 1958, and 1959 in western Washington (43); and in 1957, 1958, and 1959 in western Oregon (187) (Fig. 9).

Also contributing to the epidemiology of this region is the great variation in the grass vegetation (45, 187). Dairying is an important industry in this partially urbanized area and meadows abound in the lower, wetter soils. The grass reservoir for aphids and virus in this region is much greater than in typical grain areas; sanitation accomplished through clean tillage, summer fallow, and summer droughts is at a minimum. The culture of both winter and spring cereals in the same region also contributes to the problem.

Yellow Dwarf in the "Columbia Basin."—Yellow dwarf is known to have been a real problem in Washington (45), Oregon (106, 187), and Idaho (178), east of the Cascades and west of the Rocky Mountains in 1958. This region is subject to continental climatic factors to a greater degree than the western areas, and the winters are usually more rigorous and the summers drier and hotter. This combination subjects aphid populations to periodic reductions amounting to near annihilation. Yellow dwarf usually occurs only on very late fields of spring oats seeded on wet alluvial areas on the higher eastern fringes of the region.

In 1957-58, however, the winter was unusually mild and the spring was characterized by rains timed so as to prevent early seeding. Under these conditions, BYD developed in epidemic proportions and many late fields of barley and oats were practically total losses that year.

CONTROL OF BYD

Like epidemiology, studies on the control of BYD have only begun. The fundamental studies and field observations already extant, however, permit some treatment of various methods of control and some projection as to their ultimate value. Cultural methods designed to give the suscept every opportunity to escape infection or to tolerate infection as much as possible will be discussed, as well as the possibilities of disease control through aphid control and control through the breeding of resistant varieties.

Cultural Practices.—*Seeding date.*—Experience to date indicates that in much of the United States, spring-seeded cereals are subject to the heaviest damage when seeded late. The effect of the seeding date is often so strong that early seedings adjacent to late seedings of the same variety may yield normally while the latter fail. Farmers should be advised to seed as early in the spring as possible, but the limitations imposed by natural elements prevent this from being a dependable control practice. Epidemics have often followed springs of untimely rains that prevented tillage for considerable periods when even the best farmers were unable to seed at the recommended dates; in 1959, aphids blew northward in the Midwest in the early spring (161), making escape through early seeding impossible.

Early seeding of spring grains west of the Cascades in the Pacific Northwest (43, 187) has not been dependable as a means of lessening yellow dwarf losses in many seasons. In that region, the winters are usually mild enough to permit ovoviviparae to overwinter. The springs are cool and wet, delaying tillage but permitting aphid muliplication. Thus, when the soil has dried out to permit seeding, there is frequently a home-grown population of aphids ready to invade fields of emerging grain.

Crops from extremely early fall seedings, in the same way, are more apt to become infested with aphids and suffer from yellow dwarf. Although yellow dwarf has not been a serious problem in the major winter cereal areas, abnormally early seedings should be discouraged. Excessive rank growth of winter cereals aids ovoviviparae in overwintering (as does volunteer grain). Early fall seedings in western Washington appear more heavily infested than late fall seedings. Thus, a moderately late seeding date might have some protective value for winter cereals.

The southern areas have 1 important advantage over more northerly regions. If it is apparent that the aphids (greenbug) or yellow dwarf have destroyed a crop, there is often time to seed another crop. In many northern areas, loss of a crop is final. Nothing can be seeded to economically salvage the remainder of the season.

In much of California, seeding oats between November 15 and January 15 is recommended as aphids are most abundant in early fall and late spring, and the above period provides the greatest chance of minimizing yellow dwarf (232).

Proper seeding dates for both spring and winter cereals are well established in most of the world. They permit the crop to withstand or escape adverse

factors in the environment to the greatest degree possible. The seeding date in any given locality is relatively fixed by interaction of many variables and little future is foreseen in attempts to control BYD by alteration of seeding dates to escape aphid flights.

Seeding rate.—Some virus diseases have been partially "controlled" by increasing the number of plants/A (38). This success has been based on the occurrence of single or few flights of small numbers of vectors so that when dispersed in the crop they were so few that many plants escaped infection by the primary invaders; and with limited or no secondary infections within the field, the many escapes added to the yield. Farmers in western Washington commonly sow at the heavy rate of 3 bu of oats/A. Apparently, experience has taught them that, at least in some seasons, a greater yield is obtained from heavy seeding rates. Escape of some of the plants, at least for a time, may add to the yield in such seedings.

Plant breeders employing widely spaced plants in genetic studies in the field have often run into serious difficulty because of yellow dwarf.

Rademacher and Schwarz (183, 184) and Slykhuis, *et al.* (222) have recorded instances of reduced incidence of yellow dwarf with increased seeding rate. These observations are probably of greatest importance for persons interested in studies of aphid movements or varietal reactions in areas where heavy aphid flights do not occur. In western Washington and Oregon, where heavy aphid flights are common, no healthy plants can be found in many fields, regardless of seeding rate. Proper rates of seeding cereals, like date of seeding, are dependent on many variables, such as weed competition and moisture supply; any recommended deviation from normally established practices is not likely to be a popular and practical method for BYD control.

Observers in Iowa (41) and Michigan (134), in the epidemic of 1959, noted that yellow dwarf was most severe in "thin stands." It is not completely clear whether this thinness resulted from early infection with a virulent strain, prohibiting tillering, or if the thin stand resulted in a high proportion of infected plants. The author has observed that tillering of oats may be completely inhibited by BYD in the greenhouse, in inoculated plants transferred to fertile field soil, and in naturally infected plants in the field (Fig. 1-C). It is possible that the "thin" stand referred to above resulted from the BYD, rather than that it contributed to BYD severity.

Soil fertility.—The degree of response to improved fertility that can be expected from yellow dwarf diseased plants is not known. Oswald and Houston (167) and Allen (6) found that the root systems of diseased plants were greatly reduced. Thus, it is conceivable that improving moisture and fertility might ameliorate the depressing effect of stunted roots. Webster (262) noted that wheat on which the apple grain aphid had overwintered was yellowed and stunted on poor soil, that on highly fertile soil the aphid seemed to do little or no harm. For years, students of the greenbug have found that the cereals that were well norished tolerated the toxic material better than cereals on infertile soils (1, 29, 67, 68), even though the number of aphids/plant may be greater. Workers in Iowa (41), Illinois (127), and Michigan (134) in 1959 reported that the crop damage was much greater on infertile than on fertile soil.

Oswald and Houston, on the other hand, noted no marked response of diseased plants to improved fertility (167). They did not recommend fertility treatments as a possible means of control. The author's personal observations lead him to believe that if a susceptible variety is infected early in life with a virulent strain of virus, little can be done to induce anything approaching normal growth through fertilization (or watering).

Economic crop production is dependent on proper soil fertility. As in the case of proper seeding dates and rates, the usual recommended best agronomic practices for a region probably go as far as possible in this direction. It is probable that an adequately nourished plant not too severely diseased (somewhat tolerant, infected later, or by a less virulent strain of virus) could grow better than such a plant suffering from malnutrition as well as yellow dwarf. Experiments designed to measure the response of diseased plants to fertility levels would be of real value, but it seems illogical to look upon adequate fertility as such as a control measure.

Crop sequence and composition.—Since the BYDV is not soil-borne and is not carried in crop refuse, rotation has little direct effect on severity of the disease. Economic and ecologic factors act as strong limitations to any marked alteration in cropping sequences in major agricultural areas. But some contribution may be possible in some areas by serious study of the grasses used in meadows, ranges, or other extensive seedings. In the United States, where surpluses of cereals exist and many acres of "soil-bank" may be seeded to grasses for years at a time, such seedings should logically be made with adapted grasses that either are not hosts of the virus or are unpalatable to the aphids. Dense swards of undisturbed grass scattered through the major cereal areas could become great reservoirs of virus and aphids, and increase the problems of the farmer. Management of grasses to prevent the undisturbed multiplication of aphids, or avoiding mowing at a time when winged forms are abundant might lessen the number of migrants entering grain fields.

Maintaining a flora as varied as possible in its seasonal development could increase the level of aphid predators (145) and parasites normally present in a region. Here again, various crops probably already are grown in areas in which several important crops are adapted.

The size of the virus-aphid reservoir in comparison with the cereal acreage is highly variable and a factor in determining the abundance of locally produced vectors. In western Washington, for example, 50-75% of the cultivated areas are devoted to meadow. These meadows contain legumes and perennial grasses. When at least half of the total crop acreage is seeded to aphid-virus reservoir plants, this portion of the farming enterprise should be examined. If agronomically acceptable grasses that are immune to the virus

or are not relished by aphids could be placed in the grass-legume mixtures, they might aid in reducing the disease problem.

Aphid Control.—*Insecticides.*—Modern insecticides and efficient, quick, cheap methods of application now make the practicability of their use, as a means of controlling BYD through destruction of the vectors, an important subject for investigation. Pizarro and Arny (180, 181) used Demeton (21.2%) or Systox (mixture of 0;0-diethyl 0-2-(ethylthio) ethyl phosphorothioate) on oat plants, applied as a soil drench, foliage spray, and seed treatment. This was absorbed systemically by oats, which were rendered toxic to apple grain aphids for prolonged periods. The aphids were unable to reproduce but they were not killed rapidly enough to prevent infection by primary migrants. Such results would indicate that a tremendous primary invasion by viruliferous aphids would establish yellow dwarf in a treated field. On the other hand, if the invasion was light to moderate, such a treatment preventing reproduction and subsequent movements within the crop might result in materially reduced losses.

In Oregon, Dickason, Raymer, and Foote (75) disced surface-applied phorate (or Thimet) (0,-diethyl S-(ethylthio) methyl phosphorodithiate) and Di-Syston (0.-diethyl S-2-(ethylthio) ethyl phosphorodithiate) in granular formulations into the soil, and seeded Hannchen (spring) barley, April 16, 1959. The seedling grain was subjected to a heavy immigration of alate rose grass, apple grain, and English grain aphids. These systemic insecticides reduced the population of aphids on the grain for a time, but 100% of the barley plants showed symptoms of BYD by June 16. The treatment gave no significant difference in bushels/acre, bushel weight, or in percentage of thin barley kernels. Thus, even though the aphid infestation was reduced, no disease control resulted. In another experiment with Hannchen barley seeded May 13, 1959, similar results were obtained. In spite of soil application of granular Thimet and Di-Syston and foliage sprays of Demeton and parathion, no real control of either aphids or BYD was achieved. All plants were obviously diseased by July 6. These trials were interpreted to mean that insecticides do not offer dependable control of BYD where heavy and repeated fly-ins of viruliferous aphids occur.

In Washington, Harwood and Bruehl (118) also attempted control of BYD by the use of systemics, but only as seed treatments. Eleven organophosphorus systemic insecticides were screened in the greenhouse and field. Thimet and Di-Syston gave good aphid control for 28 days in the greenhouse. In the field at Vancouver, Wash., Di-Syston and Thimet reduced aphid populations at 24 days after seeding by 88 and 96%, respectively. Even with this degree of aphid control, however, under the conditions of heavy aphid fly-ins at this site, BYD was not controlled. All plants were infected. In a field trial with Shasta oats, seeded May 1, 1959, with plots about 0.8 A in size, neither Thimet nor Di-Syston used as seed treatments, 4 oz actual/bu, gave any measurable disease control. Kiesling (134), in Michigan, reported no demonstrable control of BYD by systemic seed treatments.

In contrast to these rather unpromising results, Caldwell, Wilson, and Schafer (52) in Indiana were remarkably successful in protecting oats with a single application of an aqueous spray of Dimethoate (0,0-dimethyl S (N-methylcarbamoyl-methyl) phosphorodithioate). It was applied May 20 and no living aphids were found in the plots for at least 2 weeks. Sprayed Clintland oats yielded 76 bu/A, whereas the adjacent unsprayed oats were destroyed by BYD.

If chemical control could be developed, it would have several advantages. Chemicals have the advantage of being applicable to almost all varieties of a cereal, of being readily available (now, rather than in 6 years or more as in breeding programs), and usable against any of the aphid species involved. They have the disadvantage of adding to the cost of producing crops. They would have to be applied at the proper time, when viruliferous aphids first begin to arrive, not after the farmer finds "noticeable" infestation. In some areas where large and repeated fly-ins might occur, as in western Washington and Oregon, it is doubtful that a single application would give reliable control. Efforts of pathologists to control leaf roll of potatoes through insecticides (218) have, for the most part, been disappointing; but sugar beet yellows (26) has been reduced through proper use of insecticides.

When the greenbug invaded Minnesota (10, 274) in early May, 1959, farmers eventually sprayed 1,000,000 A of small grain, mostly spring oats. The spray was of limited effectiveness, because of the cool weather at the time of application. Many farmers were reluctant to spray, either waiting too long or not spraying at all, because of the danger of reinvasion and because of the presence of the BYDV. In general, the results were poor. On the other hand, large-scale application of insecticides, as on 653,936 A in Oklahoma in 1950 (101), could greatly reduce the number of migrants and lessen the danger of heavy aphid infestations in the states to the north and concurrently reduce the incidence of BYD. For the greatest value of the insecticides, the epidemic would have to be foreseen, as in Indiana (208) in 1959. At any rate, realizing the full potential of insecticides in the control of BYD will require a great deal of experimentation and research.

Host resistance to aphids.—For years, entomologists and agronomists have worked toward the development of wheats, barleys, and oats resistant to the greenbug (16, 66, 146, 171, 172, 271) and corns and sorghums resistant to the corn leaf aphid (124, 171, 249). If much of the southern area of the United States were seeded to cereals that prevented the rapid muliplication of these and other vector species, the danger of migrations to the north would be greatly reduced. It has been pointed out that breeding for resistance to more than 1 species of aphid in a single cereal is a difficult task. Omugi barley (171) is resistant to the greenbug and susceptible to the corn leaf aphid. But entomologists could argue just as logically that

breeding for resistance to the virus itself is also no easy task because of its many strains.

Coon (64), in Pennsylvania, has begun a study of the ability of the rose grass, apple grain, English grain, corn leaf, and greenbug aphids to multiply on the different varieties of the World Oat Collection of the United States. This type of work might yield information that will give the pathologists substantial help in combating BYD. Endo (85), in his survey of the world collection of oats for resistance to yellow dwarf, observed disease-free plants that appeared to be escapes in some varieties. There is a possibility that these apparent escapes represented plants with an expression of lack of acceptability of the variety (or genotypes within it) to the apple grain aphid.

Control Through the Use of Varieties Resistant to the BYDV.—Cultural practices and aphid control are inadequate to accomplish complete control of barley yellow dwarf. At present, the main hope for effective control is the use of resistant varieties of the host crop. Most of the commercial varieties of oats, wheat, or barley commonly grown in the United States are highly susceptible to the BYDV. The level of resistance in these varieties of the major hosts will have to be raised by incorporation of resistance from other sources. While it is known that some commercial varieties are less susceptible than others, extensive efforts are being made to seek the highest levels of resistance in these species. Screening the world collection of cereals of the U.S. Department of Agriculture for sources of resistance is already under way and should be continued and intensified. Present knowledge of the sources of resistance, inheritance of resistance, and development of resistant varieties through hybridization are presented below. It should be kept in mind that many observations of "resistance" have not been verified. Preliminary or indicative observations are not presented in detail.

DEVELOPMENT OF VARIETIES RESISTANT TO BYD

Sources of Resistance to BYD.—Extensive efforts are being made to seek the highest levels of resistance present in oats, wheat, and barleys; and in closely related species. The results of screenings of the World Collection of Cereals of the U.S. Department of Agriculture, as well as observations of cereal performance under natural epidemics of BYD, are presented at least partially.

Barley.—More is known about BYD resistance in barley than about resistance to this disease in oats and wheat. Oswald and Houston (167) discovered a high degree of tolerance in C.I. No. 1227, 1237, 2376, and Abate (C.I. No. 3920-1). A lesser degree of tolerance was found in the commerial varieties Rojo (C.I. 5401) and Hannchen (C.I. 531). Atlas 46 (C.I. 7323), California Mariout (C.I. 1455), Arivat (C.I. 6573), and Vaughn (C.I. 1367) were intermediate, and Black Hulless (C.I. 666), C.I. 734, 998, 999, Tennessee Winter (C.I. 4633), and Club Mariout (C.I. 261) were highly susceptible. Suneson and Ramage (233) demonstrated the importance of some degree of BYD tolerance in commercial varieties in a study of comparative yields. Rojo and Velvon 11 yielded 40 bu/A, Hannchen and Kindred 28 bu, Club Mariout and Compana 16 bu, and Nepal and Bonneville only 4 bu/A in a California field trial. Schaller (209, 210, 279) has screened the bulk of the barleys in the collection of the U.S. Department of Agriculture and lists C.I. No. 3208-2, 3208-4, 3906-1, 3906-2, 3906-4, 3908-1, and 3926-3 as possessing the highest resistance yet found in California (Table 5). The most resistant barleys are all of Ethiopian origin.

Table 5. A listing of barleys reported to have outstanding resistance to BYD by 2 or more workers in the United States

Studies in	Barleys selected, C.I. No.[a]
California	
Oswald & Houston (167)	1227, 1237, 2376
Schaller (209)	3208-2, 3208-4, 3906-1, 3906-2, 3908-1, 3926-3
Wisconsin (11)	1227, 1237, 2376, 3906-1, 3906-2, 3908-1
Oregon (107)	3208-1, 3208-2, 3208-4, 3926-3, 9654, 9794
Washington (44)	3208-1, 3208-2, 3208-4, 3926-3, 9654, 9794

[a] C.I. numbers refer to accession numbers of the cereal collection of the U.S. Department of Agriculture. None of the barleys reported as outstanding is a named commercial variety.

In Wisconsin, the variety Kindred appeared more tolerant to the BYDV tban Montcalm and Wisconsin Barbless (11). Arny reported that C.I. No. 1227, 1237, 2376, 3906-1, 3906-2, 3908-1, 3947 of Etbiopia; 1429 of England; 3737 of Egypt; 6471 of Poland; and 8279 of France were superior. Orlob (159, 160) studied the effects of the virus on 2 varieties, C.I. 666 (highly susceptible) and 2376 (highly resistant). The virus was present in both. Respiration, catalase and peroxidase activity, and reducing sugar and starch contents were increased in diseased plants. Total nitrogen, nonsoluble nitrogen, photosynthesis, and transpiration were decreased in diseased plants. The changes in total nitrogen and photosynthesis in diseased C.I. 2376 (resistant) were much less than in C.I. 666 (susceptible). It appears from these

findings that tolerance is a more proper term than resistance, in measuring host reaction to BYD in barley.

In inoculation trials in North Carolina (119), Oma (C.I. 9569), Pace (C.I. 9566), and Colonial 2 (C.I. 8062) had some tolerance.

As a control measure, the resistance of commercial varieties (such as Rojo and Hannchen) is not usually dependable under severe disease conditions. For this reason, Rojo has been dropped as a source of resistance in California and it never was outstandingly resistant in Washington trials. Hannchen is considered a "fairly tolerant" commercial variety in Washington; but in a severe test at Vancouver, Wash., in 1959, it yielded only 14 bu/A. Under the same conditions, a more resistant variety (C.I. No. 3208-4) produced 70 bu (44). Foote, *et al.* (107) obtained comparable results in Oregon. Thus, it becomes evident that there are barley varieties that are highly resistant to BYD (Table 5). The fact that results of various workers are at least in fair agreement is evidence that these barleys possess resistance to a wide spectrum of strains of the virus. Apparently, therefore, the future of breeding for BYD resistance in barley is bright (272).

Oats.—Endo (85) has made the only thorough search for BYD resistance in oats. He inoculated over 4,000 varieties of oats in the field in Illinois, using the apple grain aphid as a vector for selected strains of the virus. Practically all of the varieties were highly susceptible. Among the tolerant ones, the highest type of resistance was found in *Avena strigosa* selections (Saia and others). Among the common cultivated oats, Albion (C.I. 729) was most resistant; and C.I. 4918 and Fulghum (C.I. 1915) were quite good.

Shands and Cruger (213), in Wisconsin in 1959, noted important differences in resistance to BYD among commercial oat varieties. Yields in nursery plots ranged from about 55 to 20 bu/A. Ajax, Beedee, Fundy, Garry, Newton, C.I. 7372, and 7107 seemed to have some tolerance. Shands and Cruger give an excellent review of the literature on observations of varietal reactions of oats to yellow dwarf up to this time and conclude from the literature and from their own experience that Endo's (85) test might have been too severe and that some useful tolerances among commercial varieties were obscured by it. This conclusion was supported by Arny (13), also in Wisconsin, who observed some tolerance to BYD in a dozen varieties, including C.I. No. 1012, 1050, 1364, 1436, 1963, 4664, 6668, 6954, 7010, P.C. 186606 (the preceding 3 are *Avena strigosa* types), P.I. 175526, and 180942.

Oswald and Houston (167) listed Kanota (C.I. 839) and Bond (C.I. 2733) as resistant in California. Suneson and Ramage (233), in California, found Kanota highly resistant, whereas the California Red oat was highly susceptible. In 1959, Kanota and its derivatives were listed as having some resistance in Kansas (217).

Putnam (C.I. 6927) was widely included in the nurseries of the Midwest in 1959 and it yielded well in yellow dwarf areas of Iowa (41), Indiana (51), Illinois (127), Missouri (211), and Kansas (217). For example, at Hartsburg, Ill. (127), Putnam outyielded Clintland 40 bu/A to 4. The variety Newton also showed definite value. At Doon, Iowa (41), it produced 59 bu/A; Clintland, 5.

At Corvallis, Ore., Raymer, *et al.* (188) found that Victory was as good or better than Albion in a trial of 1,000 spring oats. The varietal reactions on oats in this nursery did not correlate closely with those at Vancouver, Wash. They found C.I. No. 1833, 3071, 3228, 5032, 5207, and 5208 equal to Victory. The fact that Victory is a standard, long-time variety of western Washington and Oregon might indicate that there has been natural selection in this region for tolerance to BYD. Yet, in an inoculation trial in the greenhouse, Raymer (unpublished) found that the yield of grain of Victory was reduced 97% by BYD. In the same trial, Curt was reduced only 73%.

In Washington, Bruehl and Damsteegt (43) have begun testing 3,587 oat varieties, representing several oat species. Preliminary observations in 1959 indicated that 306 of the varieties were equally as resistant as Albion and 139 were more resistant. Victory, a common variety of western Washington, seemed to have some tolerance. This is difficult to interpret, because, in 1958, a nursery of about 20 varieties, including Victory, growing at Puyallup, Wash., was uniformly devastated by BYD. In the 1959 nursery at Vancouver, Wash., Victory was vigorous. Whether strains of the virus or environmental interactions produced this contrast is not known. Among the most promising oats in the Washington trials are Kanota (C.I. 839) and Kherson (C.I. 2871). Even though the oat prospects in general appear more optimistic than indicated by Endo's studies, it could be that under severe conditions many of the "promising" oats will fail miserably.

Additional information of resistance of oat varieties to BYD is available in the Plant Disease Reporter Supplement 262 and the 1959 Oat Newsletter.

Wheat.—For some reason, host resistance to BYD in wheat has been given much less attention than in oats and barley. Consequently, there are only a few reports dealing with varietal resistance in this crop. This might be due to the fact that wheat is damaged less than oats and barley. For example, diseased stands of winter wheat will yield surprisingly well; and spring wheat is usually seeded before oats and barley, thus delaying infection until the plants are well advanced in development. Furthermore, diseased wheat "looks better" than diseased barley or oats, even though the yields may be equally depressed (45).

Oswald and Houston (167) listed Baart 46, White Federation 38, and Ramona 50 as highly susceptible; Sonora 37 was the most tolerant. Suneson and Ramage (233) reported that California farmers avoid seeding Baart late. In their tests, the yield of Baart was reduced 56%; that of Ramona, 22% by yellow dwarf.

Waston and Mulligan (254, 256), in England, re-

ported losses in Koga II and Atle wheat from yellow dwarf. Wheats are being tested at Vancouver, Wash., but results are not yet available.

A preliminary screening of over 3,000 winter wheats at Vancouver, 1959-60, by Bruehl and Damsteegt indicated that Sun (supposedly a natural cross between Sweedish Island and English Stand-Up) and Red Russian (C.I. 4509) were quite tolerant. Both are locally adapted and recommended in western Washington, where yellow dwarf is a factor in the environment; but they are not recommended in the eastern winter wheat areas of the state. Among others of promise were C.I. No. 11230, 11234, 11236, and P. I. No. 108980 and 108981.

Smith (223), in New Zealand, reported that Fife-Tuscan had some tolerance.

HYBRIDIZATION

For the most part, existing commercial varieties of the small grains are not sufficiently resistant to BYD to constitute a dependable control. The higher resistance known to exist in some of the poorer agronomic types must be utilized through hybridization. Substantial progress has already been made in barley and oats, but so far as the author knows, no program of breeding wheat for resistance to BYD is in progress.

Barley.—The development of BYD-resistant varieties by hybridization has progressed farthest in California (279), where the disease was first recognized as of sufficient importance to warrant such efforts. Suneson (231) transferred the resistance of Rojo barley to Club Mariout by the back-cross method. The resistance of Rojo is imparted by a single recessive gene. Rasmusson and Schaller (185), also in California, have crossed the more resistant C.I. No. 1227, 1237, 2376, and Abate (C.I. No. 3920-1) with Club Mariout and Atlas (C.I. 4118). These Club Mariout and Atlas hybrids will be brought to commercial acceptance through back-crosses, but they have not yet reached this level of agronomic perfection. The 4 resistant Ethiopian barleys listed above (C.I. No. 1227, 1237, 2376, 3920-1) all possess the same single, incompletely dominant gene for resistance to BYD. Rasmusson and Schaller (185) suggest designating the Rojo gene, which is of lesser value, yd_1, and the gene of the above 4 more highly resistant varieties, Yd_2. Workers in several states (272) have barley-BYD breeding programs in progress at present (Wisconsin particularly) and before long the results of these efforts can be evaluated.

Oats.—The greatest emphasis on breeding oats resistant to BYD has been in Illinois (39, 127). It began after Endo's (85) decision that Albion (C.I. 729) was the least susceptible of the varieties he tested. Albion is a white oat of rather low yield potential and as such cannot compete among present-day varieties. Brown (39, 127) transferred the resistance of Albion to the varieties Fayette, Clarion, Newton, and Minhafer. Other good sources of resistance are being employed. Greenhouse trials and field observations to date indicate that all of the resistance of the resistant parent is transferred. In some cases, some of the offspring appear more tolerant than the resistant parent, indicating transgressive segregation. In the BYD epidemic of 1959, Albion produced 69 bu/A, and Fayette 50 bu; but the average yield of 14 selections from the cross Albion × Fayette was 80 bu/A. These results present a bright picture in the Midwest.

The preliminary results obtained in western Washington (43) and Oregon (188), however, do not augur such bright prospects as those indicated above. Albion was not particularly tolerant in these areas. Victory, an old standard variety of the area, was 1 of the best among the more than 3,000 oats present in the trials; and even it will not withstand BYD in some seasons in this area. These observations, unlike those in barley where the most resistant varieties have so far performed well in all tests, indicate important differential virus strain and host interactions. Either the resistance in oats is of a lesser level than in barley, and breaks down under severe conditions, or the individual genes for resistance afford protection to a smaller range of virus strains.

Possibly, some encouragement can be derived from the selection of Kanota as a resistant oat in California (167) and Kansas (217). This variety also performed well in an epidemic situation in Washington in 1959 (unpublished), and is 1 of the parents of Curt tbat shows good tolerance in California (9).

Avena strigosa, a diploid oat. is difficult to hybridize with common oats. It is possible that some of the yellow dwarf resistance of *A. strigosa* has been transferred to common oats by crosses of a derived tetraploid (57), C.I. 7232 (*A. abyssinica* C.D. 4549) × (*A. strigosa* C.D. 3820) × Black Mesdag, an *A. sativa* oat. Progeny of crosses of these parents segregated for resistance to BYD at Aberdeen, Idaho, in 1959 (58, 178). Zillinsky of the Canadian Department of Agriculture, Ottawa, is vigorously pursuing this hybridization approach (unpublished). To date, all *A. sativa* hybrids of *A. strigosa* tested in Washington have been susceptible.

Much progress can be made in the investigation of the BYD disease with a minimum of equipment. The major requirement is vigilance. The experimenter must be constantly alert for "stray" aphids that might bring virus to a plant on which "nonviruliferous" aphids are feeding. Otherwise, such a stray may give transmission where none should have occurred. And, if the colonies of aphids are reared on potted plants in the greenhouse, vigilance and foresight are required to anticipate the collapse of heavily taxed host plants. The human component of researches with virus, vector, and host plant is great. The author has found that judicious and faithful attendance to watering and regulation of greenhouse temperatures is requisite to success, and that the worker will be unable to absent himself for long from the experiments while they are in progress. With this note of caution, a few useful techniques will be presented.

Greenhouse Requirements and Management for Work With BYD.—Greenhouse work with BYD can succeed only when proper temperatures are maintained and adequate light provided. (The greenhouse should not average over 75°F and the light intensity should not fall below 500-600 ft-c for a 12-hour day.) These conditions strongly limit what can be accomplished in an inadequately cooled greenhouse in the summer or in a greenhouse lacking supplemental lighting in regions of cloudy and overcast winters.

The general similarity of BYD symptoms to those of malnutrition or of other adverse environmental factors necessitates the use of fertile, well-drained potting soils and proper watering. If the check plants remain deep green and vigorous, results of the inoculations can be determined with confidence; whereas, if the control plants are abnormal, interpretation of the results is difficult if not impossible. Use of high levels of fertility and as near optimum moisture as possible does not enable the host to outgrow or resist the virus, so far as the author's experience indicates.

Aphids are controlled either by sprays or fumigants. The sprays have the advantage of being applicable to a group of pots or to plants in a portion of a greenhouse. Their use, where adapted, is probably cheaper and more convenient than fumigation. Fumigants are advantageous when the desire is to destroy all the aphids in a greenhouse section. The fumigant is more likely to penetrate to all parts of the house, even under the benches, limiting the escapes materially. Fumigants (Nicofume, at least) leave little toxic residue to interfere with later experiments. A single fumigation will seldom rid plants of aphids that feed behind leaf sheaths or deep in the whorl. A regular schedule of fumigation is best when critical work is in progress.

Another facet in greenhouse studies involves the different requirements of different aphid species. The English grain and apple grain aphids thrive in the cloudy winters of Washington in the greenhouse. The corn leaf aphid has died out repeatedly and the rose grass aphid multiplied very slowly during the cloudiest periods of the year. Some other environmental factors might be responsible for these differences, but a possibility is that the 2 former aphids tolerate juices of lesser nutritive value present in plants receiving very little light.

Obtaining Nonviruliferous Aphids.—Oswald and Houston (167) found that all newly borne aphids were free of the BYDV. They obtained these nonviruliferous nymphs by placing robust, preferably wingless adults in a petri dish with a moistened filter paper on the bottom. The dish should have a closely fitting top. The adults usually do not give birth to nymphs immediately; but, by the next day, if not sooner, tiny new-borne nymphs should be found in the dish. Carefully transfer them with a fine hair brush to healthy, succulent young grain seedlings and rear them for a time in a particularly shady site that is not hot or excessively dry. The apple grain, English grain, and the greenbug aphids thrive on wheat, oats, or barley. The corn leaf aphid prefers barley; the rose grass aphid, oats or barley. Rear these colonies in isolation or cage them carefully to exclude stray aphids that might bring virus to the host plant. In addition, always maintain known virus-free plants to which you can transfer the aphids for further use.

Rochow (in correspondence) strongly urges the maintenance of nonviruliferous aphid stock colonies in a greenhouse section separate from the section containing infected plants. This isolation should give added insurance against contamination of the stock colonies, but be sure that other workers do not destroy them in routine fumigations (this has happened more than once in the author's work).

Cages.—Cages can have many variations in style and construction. Cages that fit on the top of clay pots are good. Almost all work is done with potted plants, since they are easily moved into a convenient place for transferring aphids to them or can be removed from a section while it is being fumigated. Allen (6) stapled a band of cotton in a ring to the bottom of the cage so that the cotton came into contact with the top of the clay pot. The cotton fills all the small nicks and imperfections in the rim of the pot, thus forming a seal through which aphids cannot move. This prevents them from walking into or out of the cage.

The cages should provide for watering the plants from outside. If the type of cage described above is used, it is handy to place each pot in a saucer about 1 in. deep and water by filling the saucer. One should avoid excessive watering of caged plants, because they are usually weak from lack of adequate light and are susceptible to mildew and root and crown rots. In regard to light, clear plastic screens pass more light than screens of most other materials.

Rochow prefers cylindrical cages that can be pushed down into the soil, with the plants enclosed within.

Transferring Aphids.—When individual aphids are to be moved, they should be gently disturbed first. "Tickling" them with the tip of a camel's hair brush will disturb them and they will withdraw their stylets.

Rough treament might injure their mouthparts, in which case they either die or are of limited value as vectors. This method is slow and laborious, and is used only for special, critical studies.

When a large number of vectors were required, Oswald and Houston (personal communication) shook a heavily colonized stock culture plant over slick white paper and then picked the individuals from the paper. The paper should be "slick"; it is surprising how many loose fibers project from many papers, which interfere with efforts to pick up the aphids. The white paper is useful under pots in all aphid transfers requiring care; strays are more easily detected on it than on rough or dark-colored bench tops.

Inoculating plants in plant bands for later transfer to the field is a simple process. Heavily colonized virus-source plants can be shaken lightly over the flats of plants in the 1-leaf stage to be inoculated. It is probably better to shake the source plants over them several times, as uniformly as possible, rather than to attempt inoculation by a single, heavy seeding of aphids. After several hours, or the next day, the plants should be checked to make certain there are a few aphids on each plant. It is surprising how often several aphids will congregate on a plant while its neighbor may have none. Some hand work with the brush is needed to make sure there are no plants escaping infestation by the aphids.

Leaf-Piece Technique.—The leaf piece, or split-leaf technique, is used by Rochow (191) and Watson and Mulligan (256) for acquisition feedings, and by Timian (280) for general aphid rearing as well. Rochow usually cuts a typical diseased leaf into pieces, discarding the fine tip end. The leaf pieces may be placed in separate aphid-tight and moisture-retaining containers for special studies, such as attempted virus recovery by different species of aphids, or they all may be put together in a single container. Small plastic dishes, waxed cups with tight lids, or glass vials with stoppers are suitable for this purpose. If the leaf volume is large in relation to the enclosed air space, no moisture source is usually needed. If the air volume is considerable in proportion to the leaf piece(s), a bit of moist paper will help prevent the leaf from drying out during the acquisition feed of the aphids. The aphids are removed and transferred to test plants.

This technique has several advantages. Leaves may be sent through the mail. One caging is omitted: *i.e.*, it is much easier to handle a group of vials than a group of caged plants during acquisition feeding. In studying the abilities of different species of aphids to recover virus from a given source, they may be tested simultaneously, without having them mixed up together on the source plant, requiring separation prior to transferring them to test plants. Another advantage is that, should a group of aphids used in recovery trials be contaminated and already viruliferous, the source plant will not be contaminated with the unwanted virus. The test may be repeated with nonviruliferous aphids.

In using this technique, avoid free water in the vials as much as possible; aphids become entangled in water droplets and a surprising number of them will become exhausted while struggling to extricate themselves from the droplets, and die. Watson and Mulligan (256) used moist sand to maintain humidity. A moist atmosphere is all that is required. The containers should be kept from direct sunlight.

Aphid Identification.—It is wise to submit specimens of each aphid species under study to an aphid specialist for identification in critical studies. Place a sample of the aphids in a vial containing 70% ethyl alcohol. B. F. Coons advises that the alcohol should fill the vial to reduce damage to delicate parts by sloshing in shipment. Wings are particularly useful in certain species distinctions; if no or only a few winged individuals are present in the sample, they could be nurtured for a few days at least, and possibly more aphids will become alate. A key for the identification of several common grass-feeding species has been prepared (163, 182) for use by "nonspecialists." It should be kept in mind that distinctions among the plum grain, apple grain, and bird-cherry oat aphids can only be made by aphidologists.

Feeding Aphids Through a Membrane.—Rochow (193) was able to feed the English grain aphid fluids through a membrane called Silverlight; and thus, obtain transmission of the BYDV. (Silverlight is sold by the Julius Schmid Co., 423 West 55th Street, New York 19, N. Y. A similar product is sold by Long and Long Co., 69 Roosevelt Avenue, Belleville 9, N. J., under the name, Baudruche Clear Transparent Membrane.) The juice is obtained from stem tissues of diseased oats ground in cold 10% sucrose solution. The juice is placed on the upper surface of the capping membrane which is stretched over a small chamber. The English grain aphid feeds in an upside down position. A technique of this sort should permit studies of physical properties of the virus, as well as aid in production of antisera (270).

Mechanical Inoculation of an Aphid.—Orlob (159) succeeded in transferring virus from 1 *Macrosiphum dirhodum* to another. A leg was removed at the coxa joint. The wound usually yielded a drop of haemolymph. The aphid to be inoculated was anesthetized by means of carbon dioxide and the injections were performed in a room held at 2°C. A fine insect pin (minuten nadeln) was dipped in paraffin so that more haemolymph would adhere to it. The liquid was placed on the pin and it was inserted into the abdomen of the receiving aphid. Survival of punctured aphids was usually about 90%. The rose grass aphid was not particularly efficient as a vector, but it was chosen because it was the largest. In 1 experiment, 1 of 50 injections resulted in transmission. In another, 0 of 165. When whole aphids were crushed and their juice used as the inoculum, 2 of 155 injected aphids transmitted virus [see also Day (74) and Harrison (117)].

Mueller, *et al.* (155) had remarkable success in inoculating both English grain and apple grain aphids with the BYDV. The English grain aphids, inoculated by injection, readily transmitted English grain-transmitted virus, but not apple grain-transmitted virus; and *vice-versa.* The aphids were injected between the abdomen and thorax of the dorsal surface by means of fine glass needles. About 90% survived. When 5

injected aphids were used on each test plant, crude haemolymph obtained from viruliferous English grain aphids and injected into English grain aphids resulted in 16/18 infected plants; 8/12, using clarified haemolymph; 8/20, with crude juice of infected oats; 24/24, with clarified juice; and 10/10, with partially purified EGV. Apple grain aphids transmitted AGV after injection with crude haemolymph (12/12) or with crude juice from infected oats (10/20).

Inoculation Techniques for Use in Field Experiments.—The strong influence of light and temperature on symptom expression, as well as other environmental factors, makes field experiments of great value in the study of BYD. Several workers have successfully conducted experiments in the field; some of their techniques, adapted to serve diverse purposes, are presented.

In screening vast numbers of varieties for possible resistance (tolerance) to BYD, natural epidemics provide tests of varying severity with a minimum of effort. Progress is being made in western Washington and Oregon relying on natural invasion of the test plots by flights of viruliferous aphids sufficient to bring about a general infection. This procedure has this disadvantage; there are no contiguous healthy controls. A variety unadapted to an area for some reason other than susceptibility to BYD could be penalized under such a regimen. Strips of winter cereals can be seeded in early fall through the test area to assure as nearly as possible a ready source of virus and aphids in the spring.

Suneson and Ramage (233), at Davis, Calif., used Bonneville barley seeded in October as an aphid-virus trap crop. Bonneville is a very leafy variety, susceptible to the BYDV, and relished by several aphid species. Aphids are attracted to the young, succulent Bonneville; and by December or January the test cereals are seeded. When emergence is complete, the Bonneville is cut and scattered through the test plots. The aphids walk or fly to the seedlings as the Bonneville dries up. Insecticides are used later, if needed, to reduce the aphid population. The same technique served Rasmusson and Schaller (185), also at Davis.

In Illinois, Endo (85) reared masses of viruliferous aphids in the greenhouse. In the spring, he seeded oats in spaced hills, 4 hills/variety. The greenhouse-reared apple grain aphids were largely wingless. They were transferred by hand to 2 of the 4 hills. In 2-3 days, they were destroyed by sprays and the test cereals were sprayed at regular intervals thereafter. This procedure, in the absence of large fly-ins of viruliferous aphids, gave him healthy and diseased oats side by side. This method surely entails considerable labor and management, but by it Endo was able to test the Active World Oat Collection of the U.S. Department of Agriculture (over 3,500 varieties).

Watson and Mulligan (254, 256), in England, used caged areas in fields to estimate BYD losses in different cereals. The viruliferous aphids are introduced in small areas in a field of grain, either just after emergence or at any desired time after that; the area is caged for a few days; the cages are removed; and the infested areas are sprayed thoroughly. In this manner, diseased grain developed amid healthy grain, giving a good estimate of actual losses under field conditions. In Washington, Bruehl and Damsteegt (43) attempted the reverse procedure. Cages were placed in the field after seeding but before emergence. The cages kept out migratory aphids and their progenies. The cages then enclosed virus-free cereals, whereas the surrounding oats were infected. The cages were left in place until well after heading. The enclosed oats were free of BYD symptoms, but they lacked tillers and were moderately etiolated. This procedure was considered inadequate to estimate disease losses.

Another technique where high precision is desired employs flats and 2 x 2 x 2-in. plant bands in greenhouse inoculations with subsequent transplanting to the field. Flats of plant bands and soil are steamed to destroy volunteer cereal and weed seeds and planted with the cereal or grass to be tested. After emergence, the flats of plants to be inoculated are sprinkled with viruliferous aphids. They are checked later to ascertain that each seedling bears 2 or 3 or more aphids, and aphids are placed on escaping plants with a camel's hair brush. In a few days, the aphids are removed by sprays or fumigation and the plants are transplanted to the field. The checks should be seeded in separate flats so that entire flats can be inoculated at a time. This procedure is laborious and adapted only to special tests.

Simplified Method for Transmission of the BYDV.—An inexperienced person at a small station, where no one is available to advise him, might suspect the presence of BYD, but hesitate to attempt proof by transmission studies. If aphids are present on the suspected host, proof can be particularly simple. The nymphs are born virus-free; yet, after the first day on the host, they should be viruliferous and capable of transmission. Nymphs in clusters, or aligned as they were born, could be selected as having been reared on a given plant without having moved from another plant. Transfer such nymphs to healthy seedlings (oats or barley, preferably), allow them to feed 48 hours, then kill them, and keep the plants free from other aphids. Be sure to have uninoculated plants for comparison. In about 3 weeks the inoculated plants should show clear symptoms.

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